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Black-tailed prairie dog declines in northwestern Mexico: species-habitat relationships in a changing landscape

by

Rafael Avila-Flores

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in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Ecology

Department of Biological Sciences

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To Alejandra

whose unconditional love, company and support were fundamental to finish this thesis

To my parents, Luis and Carmen

who gave me the tools to build my own way

ABSTRACT

One of the three largest systems of black-tailed prairie dog (BTPD) colonies is located in northwestern Chihuahua, Mexico. During the last two decades, the area occupied by these colonies has been highly reduced and fragmented. Previous studies suggested that agriculture, poisoning, cattle overgrazing and shrub encroachment could be the factors responsible for such declines. However, the severe drought occurring in the region between 1994 and 2004 has not been considered in this equation. Because these populations occur in arid regions at the southern edge of the species range, they could be especially sensitive to changes in plant productivity. Furthermore, fragmentation of colonies may accelerate population declines due to size and isolation effects. In this study, I analyzed species-habitat relationships at different spatial and temporal scales to understand the causes of recent declines of BTPDs in northwestern Chihuahua.

The most severe loss of colony area and most local extinctions occurred between 1988 and 2000, but most likely before 1997. Extinction of colonies before 2000 mostly occurred at small and isolated colonies in low-productivity areas. The coincidence of greatest area decline with the occurrence of most intense drought suggests a prominent role of drought in the population collapse. Overall, patterns of BTPD occurrence and abundance in Chihuahua are greatly influenced by spatial and temporal variation in forage cover. Although BTPDs were more likely to occur in open areas with short vegetation, increased forage cover positively predicted occurrence. High levels of forage cover during the dry season were positively related with BTPD density, juvenile production and population rate of change, but forage cover during the preceding rainy season was a negative predictor of demographic indices. High plant productivity during

humid periods seems to have negative impacts on BTPD populations, presumably because the rapid plant growth reduces visibility and predator detection by BTPDs. The most influential landscape variable was the effective isolation of colonies. Although increased isolation may reduce the probability of occurrence at a given site, highly isolated locations may support high population densities. Contrary to my original predictions, I did not detect significant impacts of human-related factors on BTPD distribution and abundance.

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TABLE OF CONTENTS

Chapter 1. General introduction 1

Literature cited 6

Chapter 2. Factors driving long-term changes in distribution of black-tailed prairie dogs in northwestern Mexico 10

Introduction 10

Methods 14

Study Area 14

Prairie dog colony maps 15

Land cover and vegetation maps 16

Spatial and statistical analyses 18

Results 22

Long-term changes in prairie dog distribution 22

Extinction vs. persistence within colonies 24

Extinction models 25

Discussion 27

Conservation and management implications 33

Literature cited 42

Chapter 3. Habitat selection by black-tailed prairie dogs in a disturbed landscape at the edge of their geographic range 48

Introduction 48

Study Area 53

Methods 55

Sampling design 55

Habitat variables 56

Statistical analyses 59

Results 63

Discussion 66

Management implications 75

Literature cited 81

Chapter 4. Spatial variation in demographic parameters of black-tailed prairie dogs: influence of local and landscape factors 89

Introduction 89

Methods 93

Study area 93

Demographic indices 94

Local habitat variables 96

Landscape variables 98

Statistical analyses 99

Results 102

Spatial variation in demographic parameters 102

Temporal variation in demographic parameters 105

Discussion 106

Literature cited 129

Chapter 5. General discussion 138

Literature cited 145

LIST OF TABLES

Table 2-1. Summary of changes in distribution of black-tailed prairie dogs for periods 1988-2000 and 2000-2005 35

Table 2-2. Land cover features at the beginning of each period within persistent and extinct areas 37

Table 2-3. Performance of models that explain extinction of black-tailed prairie dogs in equal-sized spatial units during periods 1988-2000 and 2000-2005 38

Table 2-4. Performance of models that explain extinction of black-tailed prairie dog colonies during periods 1988-2000 and 2000-2005 39

Table 3-1. Descriptive statistics of habitat variables measured at used and unused habitat units 77

Table 3-2. Performance of 5 hypothetical models of habitat selection by black-tailed prairie dogs in northwestern Chihuahua 79

Table 3-3. Parameter estimates of habitat variables included in the top-ranking logistic model 80

Table 4-1. Performance of 4 hypothetical models explaining spatial variation in relative density of black-tailed prairie dogs 113

Table 4-2. Performance of 4 hypothetical models explaining spatial variation in juvenile production of black-tailed prairie dogs 115

Table 4-3. Performance of 5 hypothetical models explaining spatial variation in rate of population change of black-tailed prairie dogs 116

Table 4.4. Variables in best models that explain differences in relative density of black-tailed prairie dogs 117

Table 4.5. Variables in best models that explain differences in juvenile production of black-tailed prairie dogs 120

Table 4-6. Variables in best models that explain differences in rate of black-tailed prairie dog population change 122

LIST OF FIGURES

Fig. 1-1. Record of annual precipitation in the region of Janos, Chihuahua, between 1961 and 2005 5

Fig. 2-1. Distribution of black-tailed prairie dog colonies in northwestern Chihuahua in years 1988, 2000 and 2005 40

Fig. 4-1. Distribution of sampling plots in the complex of black-tailed prairie dog colonies in northwestern Chihuahua 123

Fig. 4-2. Relationships of black-tailed dog relative density with some of the most significant variables in best multivariable models 124

Fig. 4-3. Relationships of prairie dog juvenile production with some of the most significant variables in best multivariable models 125

Fig. 4.4. Relationship between the rate of prairie dog population change and some of the most significant variables in best multivariable models 126

Fig. 4-5. Annual variation in population parameters of black-tailed prairie dogs and herbage cover in northwestern Chihuahua 127

CHAPTER 1

GENERAL INTRODUCTION

Long-term conservation of vast North American grasslands may depend on the presence and activities of prairie dogs. With their foraging activities, prairie dogs contribute to maintain open grasslands through seed removal, seedling predation, and growth suppression of woody species (Weltzin et al. 1997). Their burrowing activities have important effects on vegetation composition by modifying soil structure, nutrient cycling, and hydrology (Miller et al. 1994, Weltzin et al. 1997). Prairie dogs also provide shelter for a variety of animals and serve as food to many predators (Miller et al. 1994). Not surprisingly, prairie dog colonies harbor distinct vertebrate assemblages and may support higher animal and plant diversity compared to off-colony areas (Archer et al. 1987, Ceballos et al. 1999, Lomolino and Smith 2003).

In historical times, the most common prairie dog species, the black-tailed prairie dog (BTPD, *Cynomys ludovicianus*), occupied large continuous areas across the North American plains, from southern Canada to northern Mexico (Ceballos et al. 1993, Hoogland 1995, Miller and Cully 2001). During the past century, however, a combination of anthropogenic factors including expansion of agricultural activities, poisoning, shooting, and sylvatic plague reduced the area occupied by BTPD colonies to approximately 2% of the area occupied at the end of the 19th century (Knowles et al. 2002, Proctor et al. 2006). Currently, the IUCN considers *C. ludovicianus* "near threatened" throughout its range, and suggests that major threats to this species are habitat loss and degradation due to agriculture and livestock (Hafner 2000).

Besides direct impacts of habitat disturbances at local scales (e.g. by altering forage availability and composition), changes in spatial configuration of colonies due to habitat reduction and fragmentation may increase the extinction probability of remnant local populations. Population theory predicts that growth rates of small animal populations are more sensitive to demographic, genetic and environmental stochasticity than large populations (Shaffer 1981, Lande 1993). In addition, the extinction risk of small populations may be enhanced by more deterministic factors such as edge effects, "Allee" effects, and inbreeding depression (Hokit and Branch 2003). Similarly, high isolation among populations is expected to increase extinction risks by reducing dispersal rates, which further decreases genetic diversity, increases the rates of inbreeding, and reduces adult recruitment (Frankham 1998, Brook et al. 2002, Hill et al. 2002).

At present, one of the three largest BTPD colony complexes left in North America is found in the region of Janos-Nuevo Casas Grandes (JNCG), northwestern Chihuahua, Mexico (Ceballos et al. 1993, Proctor et al. 2006). This region includes one of the largest remnants of native grassland in Mexico, and is one of the top priority areas for conservation of Mexican vertebrate diversity (Ceballos et al. 2005). However, as occurred with most BTPD populations in North America, the extent of the JNCG complex declined to critical levels during the 20th century. The most reliable quantitative information indicates that the area occupied by colonies was reduced by about 64% between 1988 and 2000, presumably as a consequence of recent agricultural expansion, poisoning and shrub encroachment (Ceballos et al. 1993, List 1997, Marcé 2001, Ceballos et al. 2005). Overgrazing by cattle has also been considered a major disturbance factor for the prairie dog habitat in this region; in fact, substitution of the original short perennial grasses by annual grasses, forbs and shrubs has been attributed to livestock overgrazing (Desmond 2004, Ceballos et al. 2005). The one-decade long drought occurring in the region since 1994 (Fig. 1-1) further contributed to reduce plant productivity within pastures (R. List and J. Pacheco pers. comm.). Because BTPDs in Chihuahua occupy one of the driest portions of the species' geographic range (Sims et at. 1978, Facka et al. 2008), changes in plant productivity could have had significant impacts on these BTPD populations. Although population responses of BTPDs to such environmental changes are unknown, casual information from one colony suggests that prairie dog density declined from 20.9-30.7 ind/ha in 1985 (Ceballos et al. 1993) to 11.3-22.7 ind/ha in 2004 and 2005 (this study; assuming that visual counts roughly represent 45% of capture-recapture estimates as reported by Facka et al. 2008). It is unknown to what extent this pattern extends to other colonies.

Clearly, more information is required to understand the causes and magnitude of BTPD population declines in this important region. The primary role that prairie dogs play in structuring the largest native grassland ecosystem in Mexico (Ceballos et al. 1999, Ceballos et al. 2005), as well as the high potential of these populations to help the recovery of other endangered species (e.g. the current program for reintroducing black-footed ferrets; Lockhart et al. 2003), make it urgent to make management decisions that secure the long-term persistence of Chihuahuan prairie dog populations and their habitat. The ultimate goal of this research is to understand the processes behind the recent prairie dog population declines occurring in northwestern Chihuahua, Mexico, by identifying the environmental factors, both natural and anthropogenic, that influence the distribution and population performance of prairie dogs in the region. The study will address three questions: 1) What environmental and landscape factors are associated with recent changes in prairie dog distribution?; 2) What environmental and landscape factors determine current patterns of prairie dog occurrence?; and 3) What local and landscape factors are associated with spatial differences in prairie dog population performance? Together, results of this study will help to identify habitat variables necessary for the long-term persistence of prairie dogs and will suggest best management practices that are compatible with conservation of prairie dogs and their habitat.

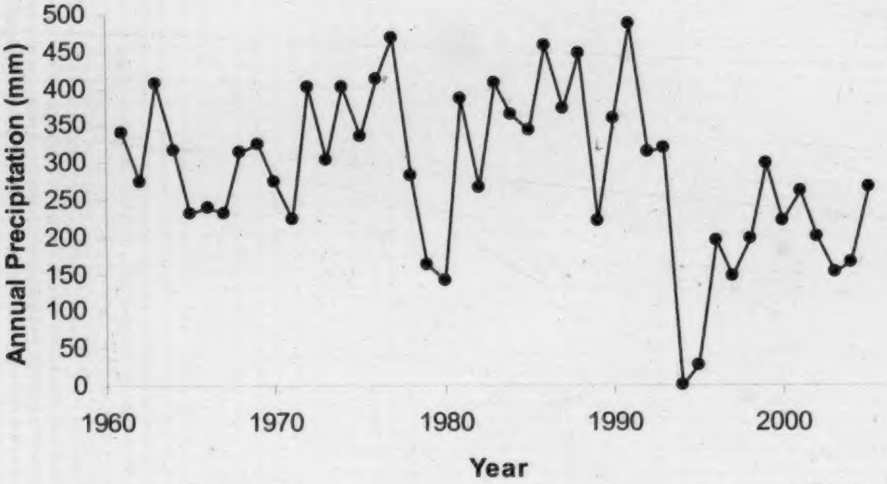

Fig. 1-1. Record of annual precipitation in the region of Janos, Chihuahua, between 1961 and 2005. The period of drought that began in 1994 extended at least up to 2005.

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CHAPTER 2

FACTORS DRIVING LONG-TERM CHANGES IN DISTRIBUTION OF BLACK-TAILED PRAIRIE DOGS IN NORTHWESTERN MEXICO

INTRODUCTION

For thousands of years, the black-tailed prairie dog (BTPD), *Cynomys ludovicianus*, has shaped the structure of extensive grassland communities throughout the Great Plains. In historical times, the BTPD inhabited vast grassland areas in central North America, from southern Saskatchewan, Canada, to northwestern Chihuahua and northeastern Sonora, Mexico (Hoogland 1995). Despite climatic and environmental fluctuations during the late Pleistocene in North America, the geographic range of BTPDs remained relatively stable over the last 40,000 years (Lomolino and Smith 2001). In the 19th century, the geographic range of BTPDs was estimated at more than 160 million ha, of which roughly 30 million ha were effectively occupied by BTPD colonies (Vermeire et al. 2004, Proctor et al. 2006). However, after European settlement in the Great Plains, BTPD populations declined rapidly until reaching extremely low levels. At present, the total area occupied by BTPD colonies is approximately 2% of the area occupied 100-200 years ago; similarly, total population numbers have declined more than 95% during the same period of time (Proctor et al. 2006, Miller et al. 2007, but see Vermeire et al. 2004). Poisoning campaigns promoted by the U.S. government (in some cases oriented towards total eradication), along with habitat loss, sylvatic plague epizootics and recreational shooting have been documented as the main causes of these population crashes (Hoogland 2006).

General decline of BTPD populations has resulted in area reduction and increased isolation of individual colonies. In the 19th century, individual colonies larger than 20,000 ha were probably common, with some exceptional colonies occupying more than 2 million ha (Knowles et al. 2002); in contrast, by the beginning of the 21st century, only five colony complexes occupied more than 4,000 ha (Proctor et al. 2006). As remnant colonies become smaller and more isolated, local populations could be more sensitive to stochastic processes and could exhibit reduced immigration rates (Hanski 1999). Such processes might further increase the extinction probability of remnant local populations and alter recolonization rates of suitable habitat patches, which could therefore compromise the long-term persistence of entire colony complexes (Lomolino and Smith 2001, Lomolino et al. 2003).

Numerical and area declines of BTPD populations are well documented for most North American regions (Proctor el al. 2006). In northwestern Mexico, BTPD populations extended over an area of 560,000 ha at the beginning of the 20^{th} century (Mearns 1907). By late 1980s, the two most important colonies in Sonora were extirpated, whereas colonies in Chihuahua were reduced to about 55,000 ha (Ceballos et al. 1993). In more recent times, BTPD colonies declined by about 64% between 1988 and 2000 in the state of Chihuahua (Marcé 2001). By analyzing area changes in a subsample of colonies, Marcé (2001) concluded that most reduction and fragmentation of colonies occurred between 1988 and 1996.

Qualitative data and casual observations suggested that agriculture, poisoning associated with cattle ranching, and secondarily shrub encroachment, were responsible for population declines in Chihuahua (Ceballos et al. 1993, List 1997, Marcé 2001). In spite of its tremendous decline in area, this system of colonies still constitutes one of the three largest BTPD colony complexes and includes the largest colony in North America (Ceballos et al. 2005, Proctor et al. 2006).

The BTPD colonies of northwestern Chihuahua occupy a desert grassland region at the southernmost limit of the species' geographic range. Available information suggests that the environmental conditions faced by southern BTPD populations may differ significantly from those faced at more northern latitudes (Facka et al. 2008, Truett et al. in press, Avila-Flores et al. submitted). Because desert grasslands occupy the driest and warmest portions of the Great Plains, they exhibit lower primary productivity as well as higher occurrence of warm-season plant species and shrubs than other North American grassland communities (Sims et al. 1978). Because optimal BTPD habitat is represented by flat open areas dominated by short-grass species (Koford 1958, Hoogland 1995, Roe and Roe 2003), BTPD populations at the southern limit of distribution could be more sensitive to reductions in plant productivity, loss of short-grass species, and increases in shrub cover. Although processes of gradual desertification and shrub encroachment have been observed in northwestern Chihuahua, presumably due to the combined effects of drought and overgrazing by cattle (R. List 1997, A. D. Davidson pers. com.), it is unknown to what extent these changes have affected BTPD distribution. Furthermore, the severe decade-long drought occurring in this region since 1994 has never been considered as a potential factor involved in the recent area decline of BTPD populations of northwestern Chihuahua.

In this chapter, I used distributional data of BTPDs for the years 1988, 2000 and 2005, in combination with remote sensing and GIS tools, to identify the environmental and landscape factors involved in the area decline of BTPD populations of northwestern Chihuahua, Mexico. I evaluated the potential roles of 1) landscape configuration (colony area and degree of isolation), 2) habitat suitability, 3) habitat loss, and 4) plant productivity, on the observed changes in distribution (extinction or persistence within spatial units) of BTPD colonies during the periods 1988-2000 (when most extreme drought occurred) and 2000-2005 (moderate drought). Due to the nature of my data, I could not objectively separate the differential effects of overgrazing by cattle and drought (through their effects on plant productivity) on extinction/persistence patterns; similarly, lack of good-quality data precluded me from evaluating the relative impacts of poisoning and shooting. I predicted that extinction within spatial units for a given period would be associated with small colony areas, increased isolation, low habitat suitability, higher habitat loss and low plant productivity. Because my study area is located in one of the driest and hottest portions of the BTPD geographic range, I expected to find a strong impact of plant productivity on BTPD distribution during the most critical period of drought (1988-2000).

METHODS

Study area

Colonies considered in this study correspond to regions I, II and III of BTPD geographic range (as defined by Ceballos et al. 1993), which encompass municipalities of Janos, Ascensión, Casas Grandes, and Nuevo Casas Grandes, at the northwest portion of the state of Chihuahua, Mexico. For simplicity, I considered all colonies in the three regions as a single complex despite the fact that several of them are relatively isolated. The study area includes the core of the proposed Biosphere Reserve of Janos, which is one of the top priority areas for conservation of vertebrates in Mexico (Ceballos et al. 2005). The region represents the northwest end of the North Plains of Mexico, and is bordered to the south and west by mountain chains of the Sierra Madre Occidental. The area is dominated by a mosaic of desert grasslands and shrublands, with interspersed patches of savannahs, riparian vegetation, agricultural lands and human settlements. Vegetation is dominated by annual forbs, annual grasses, perennial grasses, and shrubs (Desmond 2004). Climate is temperate arid with hot summers and cold winters, with extreme historical temperatures ranging from -15 to 50 °C, and a mean annual temperature of 15.7ºC; the mean annual precipitation is 307 mm, with most rains occurring from July to September and occasional snow showers in winter (García 1973). In 1994 and 1995, annual precipitation abruptly dropped to 0 and 26 mm, respectively; this extreme event marked the beginning of a period of moderate drought that extended until 2005, when mean annual precipitation was 150-300 mm (information provided by Comisión Nacional del Agua, Mexico).

Agriculture and cattle ranching are the primary economic activities of the region. In recent years, most farmers have replaced traditional farming with mechanized irrigation agriculture. Most grasslands and shrublands in private and communal lands are currently used for livestock grazing. Although some private ranches employ a grazing system of rest-rotation, most rangelands often are overstocked and exposed to continuous grazing (R. List pers. comm.). Recent declines in plant biomass production and grass abundance, increases of shrub encroachment, and acceleration of erosion processes have been considered consequences of overgrazing by cattle (Desmond 2004, Ceballos et al. 2005). However, it is unknown to what extent this desertification process was intensified by the prolonged regional drought.

Prairie dog colony maps

I used BTPD colony maps generated by G. Ceballos and colleagues (Ceballos et al. 1993, Marcé 2001) for the years 1988, 2000 and 2005. In 1988, colonies were located for the first time through ground expeditions and interviews with local people; then, colony borders (as defined by conspicuous burrows) were identified mostly through aerial surveys and drawn on 1:50,000 topographic maps (Ceballos et al. 1993). Colonies El Cuervo and Salto de Ojo were edited from original digital maps to exclude large areas covered with agriculture in 1988. In September 1999, general location of most colonies was recorded with a GPS-unit through aerial surveys. In that month, parallel straight-line plane flights separated by 1.25 km were performed to delineate the borders of the largest colony of the complex ("El Cuervo", roughly 15,000 ha by that time); after ground-verification of a small section of this colony, it was estimated that the error of aerial mapping was approximately 500 m (the same error was assumed for colony maps generated in 1988; Marcé 2001). Between September 1999 and March 2000, most of the colonies previously detected by plane were mapped on the ground, either by foot or truck, recording in a GPS-unit the coordinates of active burrows forming the boundary every 150 m (Marcé 2001). For simplicity, maps generated both in 1999 and 2000 are referred to as corresponding to year 2000. Between May and December 2005, we searched on the ground almost all colonies registered during the 1988 and 2000 surveys; during these explorations we found some colonies not registered in previous years. In the 2005 survey, all colony boundaries were mapped by foot as in 2000. For analytical purposes, colony polygons separated by < 100 m were considered as a single colony.

Land cover and vegetation maps

I gathered Landsat-5 and -7 scenes covering the study area (paths-rows 34-38 and 34-39) from the U. S. Geological Survey Global Visualization Viewer website (http://glovis.usgs.gov/). I used Landsat TM scenes of years 1990 and 1991 to describe colony attributes in 1988; Landsat ETM+ scenes from 1999 and 2000 to describe attributes in 2000; and Landsat GLS scenes (which combine ETM+ and TM data) from 2005 to describe attributes in 2005. The 3 image types had 6 visible and infrared bands and a resolution of 30 m. Metadata associated with scenes indicated that all of them were originally recorded during the local rainy season, specifically between June 17 and October 21. I used programs ENVI and ERDAS to process and classify images. Hereafter, mosaics produced with 1990-1991, 1999-2000 and 2005 scenes will be referred to as 1988, 2000 and 2005 mosaics to match the year of colony mapping. Raw or classified mosaics were used to estimate the relative primary productivity and the area covered by each land cover type within extinct or persistent colony areas.

I calculated the normalized difference vegetation index (NDVI) to produce a relative estimate of the standing-crop biomass. This widely used vegetation index uses near-infrared and red bands to estimate "greenness", producing standardized values between -1 and +1 (Jensen 2007). For practical purposes, I will use the more conventional term "plant productivity" rather than "standing-crop biomass", having in mind the distinction between the two. I produced land cover maps from supervised classifications of Landsat mosaics based on decision-tree algorithms. This method was preferred over signature-based supervised classification because it was difficult to identify unique signatures. Land cover types considered in this study were: grassland, shrubland, temperate forest, active agricultural land, inactive agricultural land, water body, barren area, and urban area. Decision-tree algorithms were produced in program See5 to classify 400-500 reference locations per year (1988, 2000, 2005) using information from an elevation model, the year-specific NDVI images, and the original Landsat mosaics (bands 2, 3, 4, 5 and 7). Land cover type of reference locations was determined directly in the field for part of 2000 (data provided by R. List) and most 2005 locations; cover type of most 2000 and all 1988 locations was defined by visual examination of satellite images based on identifiable features (towns, crops, water, prairie dog towns), unchanged habitat patches, and information provided by local people. Decision-tree algorithms were then uploaded in ENVI to classify the entire 1988, 2000 and 2005 mosaics. Final edition and filtering of raster images was performed in ERDAS, and resulting maps were converted to vector format to facilitate analyses. Overall classification accuracy of final maps was 76.8% for 1988, 77.6% for 2000, and 76.1% for 2005.

Spatial and statistical analyses

Study design.—I analyzed patterns of extinction and persistence of colony areas separately for each of two periods: 1988-2000 and 2000-2005. For analytical purposes, I only selected colonies whose distribution was known (mapped) both at the beginning (year 1) and end (year 2) of a given period (hereafter these colonies will be referred to as focal colonies). I excluded colonies that were mapped only once as well as colonies that were known at year 1 but were not properly searched on the ground at year 2. The total number of focal colonies included in analyses was 23 for 1988-2000 and 43 for 2000-2005. Hereafter, I used the term "fragment" for referring to new colonies resulting from fragmentation of a larger colony. Because the effort and strategies employed to search colonies was not consistent each year, I could not assume with certainty that colonies detected for the first time either in 2000 or in 2005 were indeed new colonies, and consequently I did not make any attempt to analyze patterns of colonization.

I identified the environmental and landscape variables associated with extinction and persistence at colony areas employing three different analytical approaches: 1) contrasting environmental conditions between portions of colonies where BTPDs became extinct with portions of the same colonies where BTPDs persisted; 2) modeling occurrence of extinction at equal-sized spatial units (cells) based on environmental and landscape attributes; and 3) modeling occurrence of extinction of entire colonies based on their environmental and landscape attributes. In all cases, colony attributes for a given period were described based on their initial conditions at year 1 rather than on their rates of change. In the case of vegetation-related attributes (NDVI value, cover of grassland, cover of shrubland, cover of barren areas), I avoided using rates of change as explanatory variables because conditions measured at year 2 could be a consequence rather than a cause of prairie dog extinction. Only anthropogenic variables (cover of agricultural and urban areas) were analyzed as rates of change because their condition at year 2 was independent of prairie dog presence or absence. All spatial analyses were performed in ArcGIS 8.1 and statistical analyses in S-Plus and Stata.

Extinction vs. persistence within colonies.—Areas of persistence and extinction were identified by overlapping maps of focal colonies delineated at the beginning and end of each period. In the resulting composite maps, overlap areas were defined as areas of persistence, whereas non-overlap (exclusive) areas corresponding to year 1 and year 2 were defined as areas of extinction and expansion, respectively. Because I was mostly interested in the problem of BTPD decline, I only focused on areas of extinction and persistence for further analyses. I overlapped polygons of extinction and persistence with NDVI and land cover maps of year 1 to describe initial environmental conditions on each. For each polygon, I calculated the average NDVI value as well as the proportion covered by grasslands, shrublands and barren lands. I used two-tailed paired t-tests to compare initial environmental conditions of extinct and persistent areas with data grouped by colony.

Modeling extinction at standard spatial units.—I created equal-sized spatial units by overlying a grid of 500 x 500 m (25-ha) cells on the study area map. Cell size was defined as a compromise between precision of colony maps (± 500 m in large colonies) and ability to properly describe features of small colonies. To define specific units of analysis, I overlaid this grid on the top of extinction and persistence polygons (as described above), and selected those cells whose area was overlapped > 50% with any polygon. Because some colonies were too small to be automatically selected by the GIS software, I selected cells by hand that included most of individual colonies (one cell per colony). In this way I obtained samples of extinction and persistence cells for each period. Then I overlapped selected cells with NDVI, land cover, and BTPD-colony maps of year 1 to describe environmental conditions and landscape context of cells at the beginning of the period. Environmental variables included: relative primary productivity (NDVI); cover of grasslands, shrublands and barren lands (ha); and absolute change (ha) in cover of (active and inactive) agricultural and urban lands. Landscape variables were: area of colony to which the cell belongs, area of colonies within 1 and 3 km, and cover of hostile area (areas potentially impeding prairie dog dispersal, in practice defined as the sum of shrubland, agricultural, forest, water and urban areas) within 1 and 3 km.

I used logistic regression analysis to model the probability of extinction of BTPDs at 25-ha spatial units (cells) by the end of each period, assigning 1 to extinct and 0 to persistent areas. I created four logistic regression models, each representing a different hypothesis of prairie dog decline, based on different combinations of explanatory variables (correlation matrix of variables is shown in Appendix I): 1) plant productivity model (NDVI values and cover of barren areas); 2) habitat suitability model (cover of grasslands and shrublands); 3) habitat loss model (change in cover of urban and agricultural lands); and 4) landscape model (all landscape variables). I used the Akaike's Information Criterion for small samples (AIC_c), ΔAIC_c and AIC_c weights (w_i) to select the model that best explain occurrence of extinction events at 25-ha cells. Pseudo-R^2 (proportion of total deviance explained by model) was calculated to evaluate overall model fit.

Modeling extinction of entire colonies.—Focal colonies were classified either as extinct or persistent for each period. Persistence was defined solely on the basis of continued presence of a given colony at years 1 and 2, not distinguishing between colony expansions or reductions. I overlapped NDVI and land cover maps with year-1 colony maps in order to describe initial environmental conditions of colonies. Environmental variables considered for this analysis were the same as in the previous section; however, because colonies varied in size, I used percent rather than absolute area of land cover types within colonies. Landscape (area and isolation) effects were estimated by including initial colony area and initial number of neighbor colonies within 3 km (from the edge of colony). I used logistic regression to model extinction of colonies separately for each period, coding 1 for extinct and 0 for persistent colonies. I compared the same four hypotheses and models as in the previous section (plant productivity, habitat suitability, habitat loss, and landscape models), and used information theoretic methods (AIC_c, ΔAIC_c and w_i) to select the most parsimonious model. The correlation matrix of explanatory variables is shown in Appendix II.

RESULTS

Long-term changes in prairie dog distribution

The total area occupied by BTPD colonies in northwestern Chihuahua declined greatly between 1988 and 2005 (Fig. 2-1; Table 2-1). By 2000, the area occupied by BTPDs represented approximately 44.4% of the area occupied in 1988, and this percentage dropped to 24.4% by 2005. As expected for this level of decline, reduction of colony area was accompanied by increased fragmentation of colonies; for example, 23 focal colonies that were recorded in 1988 resulted in 36 colonies by 2005 (Fig. 2-1). Because not all colonies were consistently surveyed in all three years, precise numbers of area change and levels of fragmentation for the entire system of colonies remain unknown. In spite of this information gap, it is clear that colony area reduction and fragmentation were noticeably higher for the first period compared to the second (Table 2-1). During the first period, 35% of focal colonies were reduced in area and 65% became extinct, but no colony was stable or extended (Appendix III); in addition, 50% of persisting colonies was fragmented (Table 2-1). During the second period 33% of focal colonies were reduced, but 30% expanded, 28% remained stable and only 9% became extinct (Appendix IV); furthermore, from the 91% of colonies that persisted, only 15% were fragmented (Table 2-1). Interestingly, extinction of colonies during the first period occurred mostly at the northern portion of the complex (Fig. 2-1). On the other hand, analyses of focal colonies indicated that the area lost to agriculture and urbanization was minimal (about 6%) for both periods (Table 2-1, Appendices III and IV), which indicates that human-caused habitat loss had a minimum role on the observed BTPD declines.

The most striking change in BTPD distribution was observed in colony El Cuervo, which was reduced from 31,497 ha in 1988 to 15,521 ha in 2000, and then to 6,255 ha in 2005. El Cuervo colony remained as a single colony until about 2000, but by 2005 it was fragmented into 10 new colonies. When El Cuervo colony is excluded from analyses, no net losses of colony area can be detected after year 2000. Indeed, whereas colony area was reduced by 67.3% during the first period, it was increased by 7.8% during the second one (Table 2-1). Correspondingly, this analytical exercise makes the average area change per colony become positive (i.e. individual colonies tended to expand) during the second period. Similarly, exclusion of the largest colony makes fragmentation less severe during the second period, as the number of fragments (new colonies) per fragmented colony was reduced from 3.7 to 2.3. Therefore, crude data clearly indicated that, except for the largest colony, the declining trend of BTPD colonies in Chihuahua had stopped by year 2000.

Although area changes in El Cuervo greatly contrast with area changes in other colonies, the causes of such great declines remain obscure. The only evident difference between extinct and persistent areas within El Cuervo is the proportion of grasslands and shrublands at the beginning of each period. At the beginning of the first period, extinct areas had 88.8% grasslands and 6.4% shrublands, contrasting with persistent areas that had 97.9% and 0.3%, respectively. During the second period, extinct areas had 87.0% grasslands and 2.9% shrublands, whereas persistent areas had 97.4% and 2.3%, respectively. Therefore, El Cuervo areas with lower habitat suitability (reduced grassland cover) were apparently more likely to become extinct.

Extinction vs. persistence within colonies

Overall, initial environmental conditions in areas where BTPDs became extinct did not significantly differ from conditions in areas of the same colony where BTPDs persisted. At the beginning of both first (1988) and second (2000) periods, areas of extinction and persistence exhibited similar NDVI values (1988: $t = 1.53$, *d.f.* = 7, $P = 0.17$; 2000: $t = 1.89$, *d.f.* = 37, $P = 0.07$), as well as similar percent cover of grasslands (1988: $t = -0.72$, *d.f.* = 7, $P = 0.50$; 2000: $t = -0.17$, *d.f.* = 37, $P = 0.87$), shrublands (1988: $t = 0.94$, *d.f.* = 7, $P = 0.38$; 2000: $t = -0.70$, *d.f.* = 37, $P = 0.49$), and barren lands (1988: $t = -0.26$, *d.f.* = 7, $P = 0.80$; 2000: $t = -0.99$, *d.f.* = 37, $P = 0.33$). Only average NDVI values at the beginning of the second period were marginally different between areas of extinction and persistence, with extinction areas having slightly higher plant productivity levels than persistence areas. However, when observations were not paired by colony, areas of persistence had (in average) a higher cover of grasslands and a lower cover of shrublands at the beginning of the period 1988-2000, but no differences were detected for the period 2000-2005 (Table 2-2).

Extinction models

In general, areas where BTPDs became extinct had a higher cover of grasslands and a lower cover of shrublands at the beginning of each period (Table 2-2). This pattern was observed at all units of analysis considered in this study, and it was especially clear during the drier 1988-2000 period (Table 2-2). Extinction of BTPDs at equal-sized spatial units was poorly explained by the four models compared in this study (no model explained > 17% of deviance; Table 2-3). Although the low explanatory power of models might indicate a failure to include more informative explanatory variables, it also could reflect inaccuracies of colony mapping and land-use classification at such a small scale. However, all model fit measures clearly indicate that the landscape model is the best to explain occurrence of extinction at 25-ha cells (Table 2-3). In both periods, probability of extinction increased with an increasing cover of hostile area (1988-2000: β-coefficient = 0.001, $SE < 0.001$, $P < 0.001$; 2000-2005: β-coefficient < 0.001, $SE < 0.001$, $P < 0.001$) and a decreasing area occupied by prairie dog colonies (for both periods: β-coefficient = -0.001, $SE < 0.001$, $P < 0.001$) within a radius of 3 km. According to the same models, occurrence of extinction during the first period was negatively related to the area of the colony to which the cell belonged (β-coefficient < -0.001, $SE < 0.001$, $P < 0.001$), but the opposite trend was observed during the second period (β-coefficient < 0.001, $SE < 0.001$, $P < 0.001$).

The higher probability of extinction in larger colonies during the second period likely results from the fact that the greatest loss of colony area between 2000 and 2005 occurred in the largest colony (Table 2-1).

Extinction models of entire colonies suggest that the landscape context was not the only factor involved in the observed decline of BTPDs colonies. Extinction of entire colonies was better modeled for period 1988-2000 than for period 2000-2005. Whereas best extinction models of the first period explained > 65% of deviance, no model of the second period explained > 20% of deviance (Table 2-4). During the first period, the landscape model included only one explanatory variable (initial colony area) because inclusion of a second variable (initial number of colonies within 3 km) did not improve its explanatory power and made estimation of model parameters very unstable. Similarly, plant productivity models in both periods had NDVI as the only explanatory variable (cover area of barren lands was excluded). For the first period the landscape model produced the best fit of data followed by the plant productivity model. However, because colony area and NDVI separately produced a relatively high model fit (each explained > 40% of deviance), I decided to produce an additional model combining both variables. This combined model improved the fit of data (Table 2-4) and showed that extinction of entire colonies was negatively related to both colony area (β-coefficient = -0.029, *SE* = 0.023, *P* = 0.201) and average NDVI (β-coefficient = -56. 283, *SE* = 34.155, *P* = 0.099). In short, these results suggest that small colonies occupying areas with low plant productivity were more likely to become extinct by the end of the period 1988-2000.

Extinction of entire colonies was poorly modeled for the period 2000-2005, as demonstrated by the low values of model performance estimates (Table 2-4). The low number of colonies that became extinct during this period (4 out of 43) is probably the cause of poor model performance. However, extinction of colonies was best explained by plant productivity as indicated by the very high AIC weight of this model (Table 2-4). In contrast to 1988-2000, extinction of colonies between 2000 and 2005 was positively related to average NDVI (β-coefficient = 52.522, SE = 26.528, P = 0.048). This model suggests that colonies with high plant productivity in 2000 (a year with close-to-average precipitation) were more likely to become extinct by 2005.

DISCUSSION

This study documents a collapse of BTPD populations in northwestern Chihuahua, Mexico, between 1988 and 2000. Although the 55.5% decline reported in this study does not exactly correspond to the 64% decline reported by Marcé (2001) (because different subsets of colonies were used in calculations), it is clear that BTPD populations exhibited a pronounced decline in area in Mexico during that period. After 2000, however, this declining trend was reversed or at least stopped (except for the largest colony which continued declining). In fact, the end of the most acute declining trend may have taken place around 1996, as suggested by distributional data of some colonies available from that year (List 1997, Marcé 2001). Although the magnitude of the population collapse observed by the end of the 20th century may have been overestimated (or even underestimated) because less precise mapping techniques were used in 1988, scattered information provided by local people and extinction of entire colonies confirms the existence of a large distributional collapse before 2000.

The relatively high degree of fragmentation observed in BTPD colonies at the study area, particularly during the period 1988-2000, could be a logical consequence of the generalized population decline that restricted individuals to increasingly smaller areas. However, because fragmentation tends to produce smaller and more isolated populations that are more likely to become extinct (Lomolino and Smith 2001), this process may have a negative feedback on BTPD distribution. In other words, once fragmentation of colonies reaches some critical level, it may accelerate BTPD population declines by increasing the probability of extinction of local populations. In the case of BTPDs, isolation effects are enhanced after fragmentation takes place because the absence of foraging activities in empty areas facilitates the development of shrublands (Weltzin at al. 1997) and other vegetation types that act as dispersal barriers. One additional problem, particularly in desert grassland areas, is that natural conversion of grasslands to shrublands is a nearly-irreversible process at the ecological time scale.

Results of this study support the hypothesis that fragmentation of colonies has facilitated the extinction of BTPDs in local areas of northwestern Mexico. Landscape variables that reflect the relative abundance and proximity of conspecifics in surrounding areas consistently appeared in the models that best explain extinction of BTPDs. At a small scale (25-ha cells), colony sites initially surrounded by a low proportion of colony area and a high proportion of hostile habitat were more likely to become extinct by the end of both study periods. At a larger scale, the initial colony size was the most important variable predicting extinction of entire colonies during the period 1988-2000, smaller colonies being more likely to become extinct than larger ones. The fact that most colony extinctions during that period occurred in the northern portion of the colony complex, where grassland patches are scarce and shrublands are dominant, suggests that isolation effects were enhanced by inhospitable surrounding areas. During the period 2000-2005, extinction of colonies was so rare that not a single variable properly explained extinction events. These findings are in agreement with extinction patterns observed in Oklahoma for the periods 1967-1989 and 1989-1997 (Lomolino and Smith 2001, Lomolino et al. 2003), which supports the idea that BTPD populations are sensitive to reduced colony size and to increased isolation (although increased isolation could indeed reduce the extinction probability of colonies in areas affected by plague; Lomolino et al. 2003). However, although size and isolation effects may explain the occurrence of many extinction events, they do not give a clue about the factors that originally caused fragmentation of colonies. Furthermore, if small and isolated colonies were more common after year 2000, why did so few of them become extinct during the period 2000-2005?

Disappearance of BTPDs from certain areas occurs because individuals die or move in response to changing environmental conditions (including human factors), and it may be a slow or fast process depending on the nature of changes. Information from the literature (e.g. Hoogland 1995, 2006, Proctor et al. 2006, Miller et al. 2007) and field observations suggest that disappearance of BTPDs from particular areas may be caused by direct kills (e.g. poisoning, shooting, road-kills), natural catastrophes (e.g. flooding), epizootic diseases (e.g. plague), loss of suitable habitat (e.g. agriculture, shrub-encroachment), or food shortage (overgrazing, drought). Because there is no historical record of unusual large-scale catastrophes or any epizootic disease (Cully et al. 2006, G. Suzán pers. comm.) in the study area, these two factors can be eliminated from the list of potential drivers of population decline. None of the remaining factors, however, can be excluded from this list. Ceballos et al. (1993), List (1997), and Marcé (2001), relying upon informal interviews with local people and detailed observations in a small portion of the complex, concluded that poisoning in private ranches, expansion of agriculture and shrub encroachment were the primary causes of the BTPD collapse in northwestern Chihuahua. Poisoning was particularly responsible for much of the colony area losses observed before 2000 in one of the largest ranches of the region (Rancho El Uno), as evidenced by the many empty poison tubes found at colony areas (Ceballos et al. 1993, Marcé 2001). However, because poisoning activities have been neither consistent nor extensive in the study area (especially in communal lands), it is unlikely that it caused the generalized collapse observed in BTPD populations. Similarly, results of this study fail to demonstrate that habitat loss due to agriculture and urbanization was an important factor causing BTPD declines.

Because suitable habitat for BTPDs is characterized by open areas with short vegetation and low cover of shrubs (Avila-Flores et al. submitted), functional habitat loss can be described as the expansion of tall herbaceous vegetation and shrubs into short-vegetation areas. The role that this type of habitat loss played in BTPD declines is difficult to evaluate because unsuitable vegetation develops in areas where BTPDs are scarce or where they have already disappeared (then the question of what caused population declines remains open). However, I found some evidence that the probability of extinction increased in areas that initially exhibited low habitat suitability. Under close-to-average rain regimes (after year 2000), BTPDs that lived in more productive areas were more likely to become extinct by the end of the study. Besides, initial habitat suitability was the only factor that could explain extinction of BTPDs in the largest colony of the complex, both before and after 2000. Within that colony, areas where BTPDs persisted had higher cover of open grasslands compared to areas of extinction. These results suggest that some colony areas suffered a gradual process of extinction, where tall vegetation and shrubs slowly invaded areas probably occupied by low-density BTPD populations.

The fact that all colonies were greatly reduced (and most became extinct) during the first but not during the second period suggests that BTPD populations were exposed to a large-scale mortality agent between 1988 and 2000. Indeed most mortality probably occurred between 1988 and 1996, as the declining process was slower after 1996 (List 1997, Marcé 2001). The coincidence of the greatest decline with the most severe period of drought (1994-1995) suggests that the reduced plant production may have affected BTPD populations. Because drought has severe negative effects on short- and long-term plant productivity

(Haddad et al. 2002), BTPDs must have been exposed to an unusually extreme, large-scale food shortage during that period. In fact, not until 2005 did plant productivity in the region approach pre-drought levels. In the scenario of most severe drought, populations living in the least-productive areas would be the most affected by food shortages. In support of this prediction, I found that initial plant productivity was one of the best predictors of extinction of colonies during the period 1988-2000, colonies in less productive areas being the most likely to become extinct. There is no doubt that extreme reductions in plant productivity during that period were enhanced by livestock overgrazing, which for decades has been a common practice in the study area (Ceballos et al. 2005). However, it is unlikely that food shortage due to overgrazing was the driving force behind BTPD declines because its distribution and magnitude is not homogenous across the region. Furthermore, overgrazing by cattle has occurred in the region even during periods of colony stability or expansion (e.g. after 2000).

Because patches of suitable habitat are probably smaller, scarcer and of lower quality at the southern edge of BTPD distribution (Proctor et al. 2006, Avila-Flores et al. submitted), populations living at these latitudes could be more affected by climatically-driven habitat changes. Although drought events might have promoted the expansion of BTPD colonies in the Great Plains (Vermeire et al. 2004); however, as plant productivity in desert grasslands is the lowest among all North American grassland types (Sims et al. 1978), extreme reductions in the rain regime are expected to have substantial negative impacts in southern BTPD populations. Indeed, it is likely that BTPD populations have historically experienced recurrent episodes of expansion and decline in response to fluctuations in climate (Forrest 2005). Climate shifts occurring in southwestern North America also seem to be partially responsible for shrub encroachment (Brown et al. 1997, Gao and Reynolds 2003), a widely documented process that is also promoted by anthropogenic factors such as grazing by cattle, fire suppression, and elimination of keystone rodents (Brown et al. 1997, Weltzin et al. 1997, Brown and Archer 1999, Curtin et al. 1999, Van Auken 2000, Gao and Reynolds 2003, Yanoff and Muldavin 2008). The dominance of shrublands in vast areas around small and remote BTPD colonies suggests that shrub encroachment has been taking place in the study area for many years. The fact that BTPDs were present in southeastern Chihuahua (400 km southeast of current geographic limits) perhaps no more than 10,000 years ago (and as far as central Mexico sometime within the Late Pleistocene; Goodwin 1995), indicates that the southern limit of geographic range has gradually been moving northward. It is likely that this range reduction has been associated with climate shifts, considering that drought events (some of them much longer and more severe) have periodically occurred in the Great Plains at least over the last 8,000 years (Woodhouse and Overpeck 1998, Clark et al. 2002). If this is true, BTPD colonies from northwestern Mexico could indeed represent relict populations that deserve special attention (but see Truett et al. in press).

CONSERVATION AND MANAGEMENT IMPLICATIONS

Results of this study suggest that BTPD populations in northwestern Mexico, especially the smaller and more isolated ones, are highly susceptible to extreme reductions in plant productivity. This vulnerability becomes critical in the scenario of global warming, as more severe drought events in arid regions are consistently predicted by general circulation models (Wetherald and Manabe 1995). Because grassland ecosystems are sensitive to all drivers of global warming, this biome is expected to suffer one of the greatest biodiversity changes within the next 100 years (Sala et al. 2000). Therefore, environmental authorities and other decision makers in Mexico should pay special attention in BTPD populations during the most severe periods of drought. The predicted negative impact of extreme drought on survival and reproduction of BTPDs could be mitigated by keeping the stocking rates of cattle at minimum levels; this action, at the same time, would reduce economic losses of ranchers because less livestock mortality would occur. In colony areas where shrubs and tall plant species are slowly replacing short vegetation, land managers can develop programs of controlled fires to maintain vegetation at the preferred early seral stages. Regional programs of management and conservation should give priority to protection of large BTPD colonies (preferably supporting the highest densities) at the center of the complex, considering that small and isolated colonies are naturally more vulnerable to environmental changes.

Table 2-1. Summary of changes in distribution of black-tailed prairie dog colonies in northwestern Chihuahua, Mexico, for the periods 1988-2000 and 2000-2005.

Colony complex attribute	Period 1988-2000	 2000-2005
Initial area (ha)[1]	44,624	19,811
Area change by the end of period (ha)[1]	-24,813	-8,932
Area change by the end of period (%)[1]	-55.6	-45.1
Area change excluding largest colony (%)[1,2]	-67.3	7.8
Average area change per colony (%)	-57.1	280.4
Number of extinct colonies	15	4
Number of reduced colonies	8	14
Number of stable colonies[3]	0	12
Number of expanded colonies	0	13
Number of fragmented colonies	4	7
Average number of resultant fragments[4]	4.5	3.7
% Area lost to agriculture	6.0	5.8
% Area lost to urban use	0.0	0.1

[1] To make numbers comparable, data were calculated from a subsample of colonies whose status was know in 1988, 2000 and 2005 (same as in Fig. 2-1); other estimates were calculated from period-specific focal colonies

[2] Colony El Cuervo, named after Ceballos et al. (1993) and Marcé (2001)

[3] Colonies that changed < 25%

[4] Only considering fragmented colonies

Table 2-2. Land cover features at the beginning of each period within spatial units of analysis used in this study. Areas of persistence and extinction are reported separately.

	Unit of analysis					
	Polygons		25-ha cells		Entire colonies	
	Persistent	Extinct	Persistent	Extinct	Persistent	Extinct
1988-2000						
NDVI	0.1	0.1	0.3	0.4	0.1	0.0
% Grassland	80.1	61.3	95.3	84.3	87.4	47.8
% Shrubland	15.8	33.0	1.7	10.3	8.2	46.0
% Barren lands	3.3	5.2	1.2	3.6	3.2	6.2
% Change agriculture (active)[1]	0.1	0.3	0.0	0.3	1.0	0.0
% Change agriculture (inactive)[1]	0.2	2.2	-1.0	4.7	6.3	0.0
% Change urban lands[1]	0.0	0.0	0.0	0.0	0.0	0.0
2000-2005						
NDVI	0.0	0.0	-0.1	-0.1	0.0	0.0
% Grassland	80.5	80.2	89.9	84.0	81.3	73.8
% Shrubland	12.4	11.9	7.4	4.7	12.3	17.0
% Barren lands	0.1	0.2	0.1	0.4	0.2	0.0
% Change agriculture (active)[1]	0.0	-0.5	0.0	0.7	-0.1	-4.3
% Change agriculture (inactive)[1]	9.1	9.1	2.1	5.0	9.0	10.2
% Change urban lands[1]	1.7	1.7	0.1	0.0	1.8	0.0

[1] Percent change in relation to initial area of spatial unit

Table 2-3. Relative performance of logistic models used for explaining extinction of black-tailed prairie dogs in equal-sized spatial units (25-ha cells) during periods 1988-2000 and 2000-2005. See text for description of variables in each model.

Model	K	Deviance	AIC$_c$	ΔAIC$_c$	w_i	Pseudo-R^2
1988-2000						
Landscape	4	2013.86	2024.08	0.00	1.00	0.113
Plant productivity	3	2222.85	2230.11	206.03	0.00	0.021
Habitat suitability	3	2116.70	2123.96	99.88	0.00	0.068
Habitat loss[1]	3	2198.72	2206.32	182.24	0.00	0.032
2000-2005						
Landscape	4	1108.40	1117.49	0.00	1.00	0.163
Plant productivity	3	1289.61	1296.24	178.75	0.00	0.026
Habitat suitability	3	1282.76	1289.39	171.90	0.00	0.031
Habitat loss[1]	3	1313.06	1319.69	202.20	0.00	0.008

[1] Change in cover of urban lands was not included because urban area was minimal

Table 2-4. Relative performance of logistic models built to explain extinction of black-tailed prairie dog colonies during periods 1988-2000 and 2000-2005. See text for description of variables in each model.

Model	K	Deviance	AIC_c	ΔAIC_c	w_i	Pseudo-R^2
1988-2000						
Landscape (Colony area)[1]	2	10.94	15.54	2.27	0.24	0.632
Plant productivity (NDVI)[1]	2	17.76	22.36	9.09	0.01	0.403
Landscape-P. productivity	3	6.01	13.27	0.00	0.75	0.798
Habitat suitability	3	20.85	28.11	14.84	0.00	0.299
Habitat loss	4	19.56	30.41	17.14	0.00	0.342
2000-2005						
Landscape	3	24.80	31.44	4.92	0.07	0.061
Plant productivity (NDVI)[1]	2	22.21	26.52	0.00	0.84	0.159
Habitat suitability	3	26.22	32.85	6.33	0.04	0.008
Habitat loss	4	22.99	32.07	5.55	0.05	0.130

[1] Univariable models

1988
N
0 5 10 20 30 40
Kilometers
2000
N
0 5 10 20 30 40
Kilometers
2005
N
0 5 10 20 30 40
Kilometers

Fig. 2-1. See description on next page.

Fig. 2-1. Distribution of black-tailed prairie dog colonies in northwestern Chihuahua, Mexico, in years 1988, 2000 and 2005. Maps only show those colonies whose distributional history was completely traced from 1988 to 2005.

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CHAPTER 3

HABITAT SELECTION BY BLACK-TAILED PRAIRIE DOGS IN A DISTURBED LANDSCAPE AT THE EDGE OF THEIR GEOGRAPHIC RANGE[1]

INTRODUCTION

The black-tailed prairie dog (*Cynomys ludovicianus*) is one of the most emblematic inhabitants of the North American Great Plains (Koford 1958, Hoogland 1995). Because of the significant role that prairie dogs play in grassland ecosystems, they are considered both ecosystem engineers and keystone species (Miller et al. 1994, Ceballos et al. 1999, Miller et al. 2000, Lomolino and Smith 2003, Kotliar et al. 2006, Davidson and Lightfoot 2006, 2008). With their foraging activities, prairie dogs not only alter the composition and structure of plant communities (Detling 1998, Royo-Márquez and Báez-González 2001, Winter et al. 2002, Davidson and Lightfoot 2006), but also help to maintain open grasslands through seedling removal and growth suppression of woody species (Weltzin et al. 1997). Burrowing activities of these rodents affect soil structure, hydrology and chemistry (Whicker and Detling 1988, Davidson and Lightfoot 2006). In addition, prairie dogs have a prominent impact on animal communities because they are the main prey for several predators and their burrows provide shelter to a variety of species (Miller et al. 1994, Kotliar et al. 2006, Davidson and Lightfoot 2007). Not surprisingly, plant and animal assemblages associated with prairie dog colonies differ markedly from assemblages found at off-colony areas (e.g. Agnew et al. 1986, Ceballos et al. 1999, Lomolino and Smith 2003), which in turn contributes to increased landscape heterogeneity and regional biodiversity (Ceballos et al. 1999, Davidson and Lightfoot 2006).

Physical and biological attributes of black-tailed prairie dog colonies are relatively well-known for areas located at central and northern portions of the species' geographic range. In general, black-tailed prairie dogs occupy open level areas at altitudes <1700 m, dominated by short- and mixed-grass vegetation, with few to no shrubs, slope <10%, herbaceous stratum <30 cm, and with deep, well-drained, silt or fine-sand loamy soils with little to no gravel (Koford 1958, Dalsted et al. 1981, Clippinger 1989, Roe and Roe 2003, Wagner and Drickamer 2004). Although these attributes presumably reflect habitat preferences of black-tailed prairie dogs (Reading and Matchett 1997), only a few studies have contrasted multiple habitat variables between used and unused sites. In these studies, habitat attributes were either measured from map layers (Reading and Matchett 1997, Proctor 1998) or were compared among few locations (Dalsted et al. 1981, Royo-Márquez and Báez-González 2001), which limits the precision of habitat descriptions and generalization of results. Adequate analysis of habitat selection at the population (or colony) level (2nd order selection according to Johnson 1980) is feasible only when comparing attributes of used and unused (or available) habitat units at multiple locations (Manly et al. 2002). In the particular case of prairie dogs, analysis of habitat selection becomes complicated by the fact that prairie dogs themselves heavily transform their habitat, particularly vegetation (Wagner and Drickamer 2004), so that conditions before settlement are unknown. However, expansion of colonies and colonization of nearby patches (which are forms of active habitat selection) occur generally at sites that exhibit characteristics similar to those of typical prairie dog habitat, i.e., short vegetation, little shrub cover, and loamy soils (Koford 1958, Milne-Laux and Sweitzer 2006, Terrall 2006, Augustine et al. 2007). Furthermore, habitat-selection studies on prairie dogs are facilitated because it is relatively easy to distinguish used from unused locations in the field (in most cases it is possible to observe individuals using specific sites *in situ*), and considering that home ranges are small, the researcher can characterize biologically relevant habitat units (Wagner and Drickamer 2004). Despite the high potential of prairie dogs as a model species for habitat-selection studies, no study has analyzed habitat variables measured in the field at multiple locations.

Because distribution and quality of resources vary over space and time, habitat selection and availability of suitable habitats may vary among populations across spatial and temporal scales (Boyce 2006). For many widespread species, both frequency of occurrence and population density decrease gradually as one moves from the center to the edge of their geographical range (Brown 1984). The reason behind this pattern is that the frequency of high-quality habitats decreases with increasing distance from the center of the geographic range, so that marginal (sink) habitats occur more often at the edge of the range (assuming that abundance and distribution are determined by a combination of environmental factors whose variability over space is autocorrelated; Brown 1984). In particular, it has been suggested that rear (southern) edge populations are typically restricted to habitat islands immersed in a matrix of unsuitable habitats (Hampe and Petit 2005). Following these hypotheses, the degree of habitat selection is expected to be high in landscapes located at the edge of a geographic range (because high-quality patches are scarcer), and the average conditions of used locations should differ between edge and central areas (because more patches of suboptimal habitat are used at the edge). Although patchy populations at the edge of the range might be more vulnerable to extinction processes acting upon small, isolated populations (Lawton 1993), and could be very sensitive to extremes in environmental conditions (e.g. Pavlacky and Anderson 2001), edge populations may be genetically more diverse and more resistant to environmental stressors than central populations (Volis et al. 1998, Hampe and Petit 2005). On the other hand, some empirical analyses suggest that, historically, edge populations have been less exposed to anthropogenic stressors than central populations (Channell and Lomolino 2000). Because of these particular traits, some edge populations might constitute priority targets of conservation efforts (Lawton 1993).

The southernmost, most-isolated complex of black-tailed prairie dog colonies is located in northwestern Chihuahua, Mexico. This is one of the largest colony complexes remaining in North America (Proctor et al. 2006), and is the core of one of the top priority areas for conservation of Mexican vertebrate diversity (Ceballos et al. 2005). Much of the region is characterized by a mosaic of shrublands and desert grasslands that intermix to different degrees (Ceballos et al. 2005), and it is mostly bordered by forested mountains and mesquite scrubs. According to recent habitat modeling exercises, this region has the lowest proportion of suitable habitat for black-tailed prairie dogs within their range in North America (Proctor et al. 2006). Heterogeneity of the region is increased by numerous anthropogenic disturbances that modify the habitat used by black-tailed prairie dogs to different degrees; overall, the region has been gradually desertified due to the combined effects of drought and overgrazing by cattle (A. D. Davidson, pers. com.). Qualitative and quantitative data suggest that changes in land-use, uncontrolled cattle grazing and shrub encroachment could be the factors responsible for the 64% reduction of the area occupied by prairie dogs during the 1988-2000 period in northwestern Chihuahua (Marcé 2001, Ceballos et al. 2005). Because these conditions differ significantly from those previously reported for other North American regions, prairie dog populations from northwestern Chihuahua are an interesting model to analyze variations in prairie dog-habitat relationships.

We analyzed patterns of habitat selection by black-tailed prairie dogs in a complex landscape of northwestern Chihuahua, Mexico. The particular objectives were: 1) to describe the characteristics of prairie dog habitat by contrasting a set of environmental variables, both natural and anthropogenic, at used and unused locations; 2) to identify the variables most strongly associated with the occurrence of black-tailed prairie dogs using a multivariable modeling approach; and 3) to quantify the degree of selectivity by prairie dogs in this complex landscape. We compared the following competing, partially nested models: 1) habitat selection as a function of physical and biological attributes; 2) habitat selection as a function of vegetation composition and structure; 3) habitat selection as a function of herbaceous layer height and shrub density, which seem to be fundamental cues for site-colonization; 4) habitat selection as a function of anthropogenic interference; and 5) habitat selection as a combination of natural and anthropogenic factors. Environmental variables were selected based on previous descriptions of prairie dog habitat and biology, and they mostly reflect habitat attributes related to food availability, predator detection, burrow construction and maintenance, dispersal facilitation, abundance of potential immigrants, interference with cattle, and potential for encounters with humans. We predicted that black-tailed prairie dogs would be highly selective due to scarcity of suitable patches, and that average conditions would be different from those previously reported for higher latitudes.

STUDY AREA

The area of study is located within municipalities of Janos, Casas Grandes, and Nuevo Casas Grandes, at the northwest end of state of Chihuahua, Mexico, approximately 20 km south of the border with the United States. The study area extends over approximately 300,000 ha at elevations between 1400-1700 m, and includes the core of the proposed Biosphere Reserve of Janos. The region represents the northwest end of the North Plains of Mexico, which belongs to the Chihuahuan Desert province, and is bordered to the south and west by the mountains of the Sierra Madre Occidental. The landscape is dominated by a complex mosaic of desert grasslands and shrublands that intermix to different degrees (e.g. to form mesquite savannas), with interspersed patches of riparian vegetation, agricultural lands and human settlements. The region is bordered to the north and east by xerophytic scrubs typical of the Chihuahuan Desert and to the west and south by pinyon and oak forests developing at Sierra Madre foothills (Ceballos et al. 1999). Climate is temperate arid with hot, rainy summers and cold winters; the mean annual temperature is 15.7ºC with extremes ranging from -15 to 50 ºC; the mean annual precipitation is 307 mm with most rains occurring from July to September (García 1973). During winter most humidity is produced by frosting, but a few snow showers and scattered rains occur.

Vegetation is dominated by annual forbs, annual grasses, perennial grasses, and shrubs (Desmond 2004). Common species in the herbaceous stratum include Indian rushpea (*Hoffmannseggia glauca*), small matweed (*Guilleminea densa*), sandmats (*Chamaesyce* spp.), spreading fanpetals (*Sida procumbens*), snakeweed (*Gutierrezia sarothrae*), Russian thistle (*Salsola kali*), blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), hairy grama (*B. hirsuta*), three awns (*Aristida* spp.), and tobosagrass (*Pleuraphis mutica*); the most common shrubs include honey mesquite (*Prosopis glandulosa*), long leaf ephedra (*Ephedra trifurca*), acacias (*Acacia* spp.), cholla (*Opuntia imbricata*), and yuccas (*Yucca* spp.) (Royo Márquez and Báez González 2001, Desmond 2004, R. Avila-Flores and A. de Villa-Meza unpublished data). At a national scale, the region supports a high number of threatened species of vertebrates, provides primary breeding and wintering habitat for many grassland birds, and is one of the top priority areas for conservation of mammals (Ceballos et al. 2005, Manzano-Fischer et al. 2006).

Signs of human activity are evident across the entire landscape in the study area. Virtually all communal (*ejidos*) and private (ranches) lands are used either for agriculture or cattle ranching, which constitute the primary economic activities of the region. In some areas, local economy is strongly driven by Mennonite groups, which in recent years have substituted traditional farming with mechanized irrigation agriculture. Most grasslands and shrublands are currently used for livestock grazing; whereas private ranches often employ a grazing system of rest-rotation, communal lands are often overstocked and exposed to continuous grazing (Desmond 2004). Previous studies suggest that heavy grazing is the primary cause of recent declines in plant biomass production and annual-grass abundance, as well as a factor that promotes shrub encroachment and accelerates erosion processes (Desmond 2004, Ceballos et al. 2005). However, it is likely that this impact has been intensified by a recent decade long drought event; vegetation data from 2004-2007 shows that annual and perennial grasses became more abundant once the annual rain volume reached average levels (R. Avila-Flores unpublished data). Drought events, in combination with increased illegal drilling of wells for irrigation agriculture, have resulted in low levels of underground water (Ceballos et al. 2005).

METHODS

Sampling design

Study design was type I according to Manly et al. (2002), i.e., resource (habitat) selection is inferred at the population level by taking random samples of habitat units across the entire study area. We employed a case-control sampling protocol, where random samples of used and unused habitat units are taken independently (Manly et al. 2002, Keating and Cherry 2004). Used and unused areas were defined before sampling based on local maps of prairie dog distribution. Colony maps were produced in 2005 after an intensive survey conducted in the study area, in which GPS readings were taken by foot at borders of all known colonies (most data provided by G. Ceballos and colleagues). We used ArcGIS 9.1 to create 7-km buffers around each colony. Then buffers were merged into one polygon to define the area over which non-use could be estimated. We set the limit of buffer areas at 7 km because this is the maximum linear dispersal distance estimated for black-tailed prairie dogs (Garrett and Franklin 1988, Hoogland 2006). Two independent sets of random points (center of habitat units) were generated, from which we sampled 151 used and 133 unused habitat units. The size of habitat units was set at 0.25 ha (50 × 50 m), which is approximately the average territory size (0.3 ha) of prairie dogs (Hoogland 1995). The entire study area contained 1,090,488 unused and 59,724 used habitat units.

Habitat variables

Randomly selected habitat units were characterized by a number of environmental variables expected to affect the probability of occurrence of prairie dogs. The first set of habitat variables was measured directly in the field during the peak of plant productivity, between August 11 and September 21, 2005; that year the annual precipitation was 267 mm, which is lower than the multi-annual mean but is still within the range of variation of pre-drought years. Sampling was complete by the time the rains became scarce and the herbage showed signs of death (dryness of leaves). During that period, we accessed each of 283 habitat units by vehicle and foot. At each sampling point we placed two 50-m perpendicular, crossing ropes, centered at the coordinates of random point locations. Samples taken at the center or along these line transects were assumed to represent an effective area of 0.25 ha (50 × 50 m). At each habitat unit, we confirmed that the site was used or unused, and recorded the following parameters: altitude, slope, texture of soil, vegetation type, density of cattle droppings (as a measure of the level of cattle activity), shrub density and cover, height of herbaceous stratum, and percent cover of shrubs, grasses, forbs, woody/spiny/sticky weeds, dry vegetation, and barren ground.

Use and non-use were clearly distinguished because used sites had conspicuous burrows with evident signs of activity (fresh prairie dog feces, open entrances, or soil removed on mounds); in most cases, used locations were confirmed by direct observation of active individuals. We recorded the altitude at the center of habitat units using a GPS unit and the dominant slope with a clinometer. Texture of soil (rocky, sandy, silty, clay, or mixed) was qualitatively determined by touch, always by the same person to minimize observer variability. Vegetation type was recorded either as grassland, open shrubland, semi-open shrubland, closed shrubland, chaparral, riparian vegetation, or crop. Density of cattle droppings and density of shrubs taller than 50 cm (including yuccas, chollas and cactus) were estimated by counting the number of cattle droppings and shrub stems, respectively, that fell within two belt transects (2-m wide) centered at the two 50-m line transects; in both cases, density was standardized as number/ha.

We used the line intercept method to estimate the percent canopy cover of shrubs along line transects (Canfield 1941). The dominant height of herbaceous stratum was estimated visually as a range, but only the mid-point of the range was used for statistical purposes. The percent cover of grasses, forbs, mature woody/spiny/sticky weeds, standing-dead (dry) vegetation, and bare ground was visually estimated within square frames of 50 × 50 cm (with strings attached at 5-cm intervals to form a grid of 100 small squares) that were placed at 5-m intervals along the two transects; the average percent for each category was used for statistical analyses (n = 20). Hereafter, woody/spiny/sticky weeds (e.g. mature individuals of *Amaranthus palmeri*, *Gutierrezia sarothrae*, *Salsola kali*, *Solanum eleagnifolium*), which were assumed to be avoided by prairie dogs, will be referred to as unpalatable vegetation.

The second set of habitat variables were extracted from digital maps using ArcGIS 9.1. At the central point of habitat units, we extracted: type of soil (feozem, litosol, regosol, vertisol, xerosol, yermosol, or others), size of soil particles (fine, medium, large), moisture regime of soil (aridic with <90 days of moisture, xeric with 90-180 days of moisture, or ustic with 180-270 days of moisture), area covered by prairie dog colonies within circular buffers of 1 and 3 km, area covered by hostile habitat (i.e., habitat potentially impeding dispersal movements of prairie dog individuals) within circular buffers of 1 and 3 km, road density (in meters) within circular buffers of 1 and 3 km, and linear distance to nearest main road and to nearest town. We employed the National Forest Inventory (IFN) map produced by the Mexican government (SEMARNAP-

INEGI-UNAM 2001) to quantify land cover variables. Maps describing soil characteristics as well as road maps were obtained on-line from the website of *Comisión Nacional para el Conocimiento y Uso de la Biodiversidad* (CONABIO; Maples-Vermeersch 1992, INIFAP-CONABIO 1995). The map of main roads was generated by selecting on the original map only those paved or dirt roads that in our experience are the most heavily used by vehicles in our study area. Hostile habitat was measured as the sum of area covered by water bodies, shrublands, woodlands, agricultural lands, and urban areas.

Statistical analyses

Univariable descriptive analyses.—We used both parametric and non-parametric tests to illustrate the magnitude of differences in individual habitat variables between used and unused sites. For categorical variables, we used the Pearson's Chi-square test of independence to determine whether the use of different categories was proportional to their availability. Continuous variables originally expressed in units of area, density/ha or length were log (ln) transformed for normalization, whereas variables originally expressed as percentages were arc-sin transformed. We used two-sample *t*-tests to determine whether individual habitat variables differed between used and unused habitat units. For most habitat variables, however, we used the Welch modified two-sample *t*-test for unequal variances because the variance of unused habitat units was higher than that of used units. Significance was determined at the conventional level of 0.05. We used S-Plus 7.0 to perform univariable statistical analyses.

Multivariable model building.—We used multiple logistic regression to identify the set of habitat variables most strongly associated with occurrence of prairie dogs. Model building was performed in S-Plus and Stata. We used the raw (untransformed) data to perform all modelling exercises; moisture regime was treated as an ordinal (rather than categorical) variable to reduce parameterization. Because all habitat variables were originally selected based on knowledge of prairie dog natural history, we decided to include all variables in the first stages of the modeling process. The only effort we made to select variables consisted of the elimination of redundant variables to reduce collinearity. From a given pair of variables that had a correlation coefficient ≥ 0.7 (Appendix V), we eliminated the variable that produced smaller differences between used and unused areas (higher P-value) after performing two-sample t-tests and univariable logistic regression analyses. Because we had biological reasons to believe that some variables (e.g. height of herbage layer, incidence of cattle) might exhibit non-linearities in their relationships with prairie dog occurrence (e.g. Clippinger 1989), and that some pairs of variables (e.g. cover of grasses and cover of forbs) might have interacting effects, we tested the importance of quadratic and interaction terms using separate logistic regression analyses. We excluded non-linear and interaction terms from the final multivariable models because of their low individual explanatory power. Exclusion of less influential redundant variables, as well as of non-linear and interaction terms in final models, also was justified by the high standard errors and low t-values exhibited by their β-coefficients in the initial global models.

We built five groups of multivariable logistic models to test five hypotheses of habitat selection: 1) occupancy as a function of biophysical environmental variables, 2) occupancy as a function of vegetation variables, 3) occupancy as a function of herbage height and shrub density (visual obstruction), 4) occupancy as a function of human interference, and 5) occupancy as a function of a combination of biophysical and anthropogenic factors. Although the area covered by hostile habitat in the surrounding landscape results from a combination of natural and anthropogenic land cover types, this variable was included in the anthropogenic models because most of that area consists of agricultural and urban lands (58%); another 40% of hostile area is occupied by shrublands, a proportion of which might have resulted from human-induced shrub encroachment (Ceballos et al. 2005). We produced two types of models to represent hypotheses 1, 2, 4 and 5: one model including all variables (global) and one more parsimonious model (best subsets). Variables in the global model of hypothesis 5 were selected based on best subsets of models 1 and 4. We selected the best subset of variables from each global model based on the likelihood version of Mallow's *Cp* statistic, which in linear regression context is a measure of the predictive squared error of individual variables (Hosmer and Lemeshow 2000). At each step in the best subsets process, the program eliminated the variable whose exclusion in the model produced the lowest *Cp* value, until no additional droppings were required to reduce the *Cp* value of the precedent (more parameterized) model. In total, we produced 9 competing models to evaluate 5 different hypotheses of habitat selection.

We employed information-theoretic methods to select the model that best explained habitat occupancy among the 9 candidate models. Because the number of parameters of some models was relatively large in relation to sample size, we ranked models according to the Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). We calculated ΔAIC_c, w_i (AIC weight), deviance, and pseudo-R^2 (a simple measure of the proportion of total deviance explained by model) to provide additional measures of model fit (Burnham and Anderson 2002, Hoffman 2004). The model chosen as the best, given our data, was that model with the lowest AIC_c value, provided that no other model had a $\Delta AIC_c < 2$ or similar w_i score. We confirmed the significance of β-coefficients in the final model by evaluating the magnitude of associated standard errors and the value of Chi-squared Wald statistics. The overall performance of the best model was evaluated by estimating the area under the ROC (Receiver Operating Characteristic) curve. The ROC statistic uses two measures of correct classification, sensitivity and specificity, to assess the capacity of models to fit and discriminate data (Hosmer and Lemeshow 2000).

Quantification of selectivity in the context of landscape.—In heterogeneous landscapes where habitat units of high quality are scarce, we would expect individual animals exhibiting a strong degree of habitat selectivity in relation to total availability. If this is true, we could predict that characteristics of used and unused habitat units would be clearly different in such landscapes, and that the expected probabilities of use resultant from a modeling exercise would differ significantly between samples of used and unused units. To quantify the level of selectivity by prairie dogs in the context of the heterogeneous landscape of northwestern Chihuahua, we compared the average probability of use between used and unused habitat units. We used our best logistic regression model (see previous section) as a resource selection probability function (RSPF; Manly et al. 2002) to calculate the expected probability of use for each of our sampled habitat units. Because logistic regression is not appropriate to calculate the conditional probability of use in studies employing case-control designs (Manly et al. 2002), we used the adjustment suggested by Keating and Cherry (2004) to account for the bias in the proportion of used and unused habitat units in our sample. We calculated P_1, the proportion of habitat units that were sampled within the total universe of used habitat units in our study area (151/59,724), and P_0, the proportion of habitat units that were sampled within the universe of unused habitat units in our study area (133/1,090,488). Then, by subtracting the natural logarithm of P_1/P_0 from the linear predictor in the logistic regression equation, we were able to calculate the expected probability of use for each sampled habitat unit. To quantify the degree of habitat selectivity, we compared the expected probability of use between used and unused locations, assuming that the magnitude of the difference would provide information on the magnitude of selectivity based on sampled units.

RESULTS

Descriptive statistics of individual habitat variables show that prairie dogs occupy sites that encompass a relatively broad range of environmental conditions (Table 3-1). Univariable statistical tests revealed that sites occupied by black-tailed prairie dogs tended to have lower slopes, lower content of sand and rocks in soil, shorter herbaceous vegetation, lower density and cover of shrubs, lower percent cover of grasses and unpalatable vegetation, and higher percent cover of bare ground, as compared to unused sites; prairie dogs tend to be absent from sites with feozem and litosol soils, with a low proportion of prairie dog colony area within 1 and 3 km, and with a high proportion of hostile habitat within 1 and 3 km (Table 3-1). We did not detect significant differences between used and unused habitat units in relation to altitude, soil moisture regime, incidence of cattle, cover of forbs, cover of standing-dead vegetation, road density within 1 and 3 km, and distance to main roads and towns (Table 3-1).

Multiple hypotheses testing revealed that biophysical habitat variables had a much stronger influence on habitat selection than anthropogenic factors (Table 3-2). Although the most parsimonious model (top-ranking model according to AIC_c) was a composite model that included 1 anthropogenic variable in addition to 8 biophysical variables, the biophysical model with 10 habitat variables performed almost as well as the composite model ($\Delta AIC_c = 2.74$). Both vegetation and visual obstruction models, which are nested submodels of the global biophysical model, performed relatively well in comparison to the human-impact model (Table 3-2).

The most parsimonious model explained about 63.4% of total deviance of data, which is just slightly lower than the proportion explained by the two most parameterized models, and obtained the strongest support among competing models based on its w_i score (Table 3-2). The area under the ROC-curve for this model was 0.964, which indicates an "outstanding" discrimination power of the model (Hosmer and Lemeshow 2000). Using a cutoff point of 0.5, sensitivity (proportion of used habitat units correctly predicted to be used) was 91.39%, and specificity (proportion of unused habitat units correctly predicted to be unused) was 87.22%, with an average of 89.44% of correct classification. All β-coefficients in the model had relatively small standard errors and confidence intervals did not overlap with zero.

According to the most parsimonious model, the probability of use of habitat units by prairie dogs is directly proportional to the moisture level of soils, percent cover of forbs, percent cover of unpalatable vegetation, percent cover of bare ground, and amount of prairie-dog colony area within 1 km, and inversely proportional to altitude, density of shrubs, height of herbage layer, and amount of hostile area within 1 km (Table 3-3). Of these, the four most significant habitat variables (according to Wald statistics) were, in order of importance, herbage height, shrub density, cover of unpalatable vegetation, and altitude. The primary role that herbage height and shrub density have on prairie dog habitat selection is demonstrated by the relatively good performance of the visual obstruction model, which with only two variables explained 53% of total deviance (Table 3-2). In particular, the odds a habitat unit is used by prairie dogs decreases to 0.75 and to 0.999 with an increase of 1 cm in herbage height and with the addition of 1 individual shrub per hectare, respectively (Table 3-3). Some habitat variables that were non-significant in univariable tests were very important in the global as well as in the most parsimonious model. In particular, effects of soil moisture, altitude, and cover of forbs were detected only when the effect of other variables was controlled.

Differences in expected probabilities of use between sampled used and unused habitat units revealed that prairie dogs exhibit a relatively high degree of selectivity of habitat units within the landscape. Using unadjusted fitted values, the average probability of use for unused habitat units was 0.162 (± 0.256), whereas the average probability of use for used habitat units was 0.858 (± 0.202). After adjusting fitted values to reduce the effect of sampling bias, the actual average probabilities of use were reduced to 0.026 (± 0.067) for unused habitat units, and 0.425 (± 0.257) for used units. The 95% confidence intervals surrounding these estimates do not overlap. The relatively low probabilities of use after adjustment of fitted values reflect the fact that suitable habitats are relatively scarce in the landscape. The large differences in expected probabilities of use between used and unused habitat units reflect that prairie dogs are selecting sites that differ from most available locations.

DISCUSSION

Black-tailed prairie dogs living at the southernmost edge of the species' geographical range use sites that encompass a relatively broad range of environmental conditions. However, despite the apparent flexibility in habitat requirements, prairie dogs of northwestern Chihuahua use sites that greatly differ from most unused available sites. In this mosaic of croplands, urban settlements, range-grasslands, shrublands, mesquite savannas, and riparian areas, prairie dogs prefer sites that are similar in many respects to sites used by prairie dogs in more northern locations. Prairie dogs of Chihuahua most frequently use sites located in flat open areas with low visual obstruction, at altitudes <1600 m, with texture of soils ranging from fine to medium, and with a relatively high proportion of surrounding area occupied by prairie dog colonies, such as has been reported for more northern locations (Clippinger 1989, Reading and Matchett 1997, Proctor 1998, Roe and Roe 2003). Using multivariable analytical tools we found that height of herbaceous stratum and shrub density (both variables related to the degree of visual obstruction) were the most important factors affecting habitat selection by prairie dogs in this heterogeneous landscape.

Previous descriptions of prairie dog habitats suggest that soil properties are probably the most important components of the physical environment. Although prairie dogs occupy a variety of substrate types (Clippinger 1989), they seem to prefer deep, well drained, silty or loamy soils with moderate content of sand and little to no gravel (Clippinger 1989, Reading and Matchett 1997, Roe and Roe 2003). Furthermore, these features appear to be generalized among prairie dog species, considering that similar soil conditions have been reported for *C. gunnisoni* and *C. mexicanus* (Treviño-Villarreal et al. 1997, Wagner and Drickamer 2004). According to our results, black-tailed prairie dogs from northwestern Chihuahua use soil types in proportion to their availability, but they tend to avoid rocky soils that are rich in organic matter (feozem) as well as shallow soils (< 10 cm deep) developed on top of rocky matrix (litosol). Although our qualitative measures indicate that sites used by prairie dogs are dominated by soils of fine or medium texture, quantitative information collected in 48 additional locations indicate that sandy soils (50-80% of sand content) are common within prairie dog colony areas (R. Avila-Flores unpublished data). These results are supported by an independent study conducted in 4 paired locations at the same colony complex, which found that sand content was about 60% both within- and off-colony areas, with lower content of organic matter within colonies (Royo-Márquez and Báez-González 2001). On the other hand, moisture regime is the only soil property consistently present in our most parsimonious multivariable models, which suggests that moisture is the most relevant soil property once the effect of other important habitat variables is controlled. In other words, when comparing sites that are similar in relation to shrub cover and herbage height (plus other 6 minor variables), prairie dogs are more likely to occur in sites that have more humid, presumably more productive soils. In short, southern populations of prairie dogs seem to be able to use a variety of soil types as long as they can support burrow systems, and no clear patterns of soil selection emerge from our analysis.

Two other important physical components of prairie dog habitats are slope and altitude (Hoogland 1995, Roe and Roe 2003). Although we found a significant difference in slope between used and unused locations, the influence of slope on site occupancy was diluted when we introduced other variables into multivariable models. These results contrast with those of previous studies employing multivariable modeling approaches, where best models included slope or slope variability as one of the most important variables predicting prairie dog occurrence (Reading and Matchett 1997, Proctor 1998, Wagner and Drickamer

2004). After a comprehensive literature review, Clippinger (1989) identified slope as one of the four most important habitat variables in a habitat suitability index for black-tailed prairie dogs, because flat areas are usually associated with broader visual fields. Although previous multivariable modeling approaches used less accurate slope data extracted from maps, they consistently showed prairie dogs exhibiting a strong selection for sites with slopes <10%. This is consistent with our data and with published information that was collected in the field (Clippinger 1989, Roe and Roe 2003), which indicates that black-tailed prairie dogs rarely occupy slopes >20%. We believe that slope did not predict occurrence in our multivariable models because flatness was a prevalent characteristic across most locations in the study area including unused locations. In contrast to slope, altitude alone was not significantly different between used and unused locations and still emerged as an important variable in the most parsimonious multivariable models. Although elevation has not been included as a covariate in previous multivariable modeling efforts, it might indeed be an important habitat feature because prairie dogs have never been found above 1,700 m (Hoogland 1995). In our study area, increases in altitude are closely associated to increases in topographical complexity, so that locations above 1,500 m tend to be located over steep or undulated terrain surrounded by cliffs, hills and mountains. Therefore, the scarce suitable locations found at high altitudes might be less likely to be occupied by prairie dogs due to the increased occurrence of topographical dispersal barriers.

According to previous studies, the percentage of herbaceous cover on prairie dog colonies ranges between 25 and 91%, and it has been suggested that for continuous habitation it should never be <15% (Clippinger 1989, Roe and Roe 2003). The strikingly low percent cover of grasses and forbs reported in this study during the productive rainy season (very often <15%), both on- and off-colonies, suggests that food abundance is probably one of the most limiting factors for prairie dogs at the southernmost edge of distribution. This conclusion is consistent with the fact that desert grasslands have the lowest primary productivity among all North American grasslands (Sims et al. 1978). Indeed, we found that prairie dogs are more likely to occur on sites that have a higher cover of forbs once the influence of other variables is controlled. The positive association between bare ground cover and prairie dog occurrence in multivariable models can be explained by the tendency of prairie dogs to avoid highly productive sites during the rainy season and by the heavy reduction of grass cover (presumably due to foraging) within colonies. Likewise, high incidence of unpalatable vegetation in used locations could be a consequence of prairie dog presence rather than a selected habitat feature. Although unwanted plant species are actively cut by prairie dogs (Hoogland 1995), annual and invasive weeds could colonize disturbed areas with sparse vegetation (as in prairie dog colonies; e.g. Davidson and Lightfoot 2008) so rapidly during the rainy season that prairie dogs are unable to cut all of them. Alternatively, but less likely, some of the plant species considered here as unpalatable may indeed be used by prairie dogs as a source of food, as has been reported for immature Russian thistle and amaranths (Koford 1958, Davidson and Lightfoot 2008).

Although low vegetation height and reduced visual obstruction have been recognized as prominent features of prairie dog habitat (Koford 1958, Clippinger 1989, Hoogland 1995, Roe and Roe 2003), limited quantitative information supports this assumption. Here we report strong evidence suggesting that site occupancy is mostly determined by low herbage height and shrub density. Available information indicates that dominant herbage height in more northern colony areas ranges between 2 and 30 cm (Koford 1958, Agnew at al. 1986, Archer et al. 1987, Hoogland 1995, Winter et al. 2002, Pauli and Buskirk 2007), and it has been suggested that 5 cm is the minimum height for viable herbage cover (Clippinger 1989). Although most used locations in this study exhibited an average plant height within that range, we often found prairie dogs occupying sites with vegetation shorter than 2 cm. Indeed we did not find evidence of a minimum herbage height required for site occupancy, as demonstrated by the lack of any quadratic relationship between herbage height and prairie dog occupancy. On the other hand, the primary role that shrub density and cover play in habitat selection seems to be restricted to areas located at the southern edge of prairie dog geographic distribution, where shrublands and grasslands may form heterogeneous mosaics. The virtual absence of shrub data in previous habitat descriptions suggests that shrubs are infrequent in most prairie dog colony areas. An exception comes from a study conducted in north-central Texas, where the percent canopy cover of mesquite was as high as 27% (measured in aerial photos) during a year of prairie dog eradication (Weltzin et al. 1997); it contrasts to shrub covers <2% reported for colonies of north-eastern Wyoming (Pauli and Buskirk 2007). In northwestern Chihuahua, despite the relatively high incidence of shrublands in the landscape, the average shrub cover measured at used locations was only 0.3%. However, prairie dogs exhibited some flexibility in shrub tolerance, as they occurred in sites with shrub covers as high as 10.6% and with shrub densities >2,000 shrubs/ha.

Herbage height and shrub density measured at used locations partially result from clipping and foraging activities of prairie dogs (Osborn 1942, Koford 1958, Weltzin et al. 1997), which would indicate that the patterns reported here are a consequence of prairie dog presence rather than active habitat selection. However, some indirect evidence suggests that short vegetation and reduced shrub density are indeed actively selected by dispersing prairie dogs. Anecdotal observations indicate that many tall-grass and highly productive areas can be colonized by prairie dogs only through facilitation by livestock grazing (Osborn 1942, Koford 1958, Knowles 1986), and it has been suggested that overgrazing by cattle and drought events were the most important factors causing the colony expansions in the late 1800s (Vermeire et al. 2004). Similarly, we anecdotally observed how prairie dog individuals shifted territories from a ranch with no cattle to an adjacent pasture grazed by cattle as soon as a dense herbage layer developed after the first summer heavy rains. On the other hand, more specific studies suggest that dispersing individuals move through routes that offer little visual obstruction and select territories that have low vegetation (Knowles 1985, Roach et al. 2001). In addition, it has been experimentally demonstrated that controlled grassland burns, herbage mowing and mechanical shrub removals significantly increase rates of colony expansion (Milne-Laux and Sweitzer 2006, Augustine et al. 2007, Northcott et al. 2008), and that dispersal movements of prairie dogs may be effectively restrained by vegetation barriers taller than 40 cm and wider than 85 m (Terrall 2006).

We found little evidence that anthropogenic features influence significantly habitat occupancy. However, the negative relationship between habitat occupancy and amount of hostile habitat within 1 km suggests that habitats created by humans may indeed create barriers for dispersal. In accordance with this conclusion, the positive relationship between habitat occupancy and amount of colony area within 1 km suggests that the number of potential dispersers in the surroundings may affect the colonization process. Our results suggest that the effective area occupied by anthropogenic dispersal barriers (crops, towns, encroached shrubs) is more efficient to predict site occupancy than direct encounters with humans near roads or towns. In reality, mortality events directly caused by humans (poisoning, shooting, roadkills, feral dog kills) are rarely observed in our study area. The lack of negative relationships between site occupancy and potential human encounters has been reported in previous studies. In Montana, occurrence of prairie dog colonies was positively associated with homestead sites (Knowles 1986), whereas prairie dog density and colony size were not related with distance to roads (Reading and Matchett 1997). In Colorado, burrow density was found to be positively related with road density

(Johnson and Collinge 2004). On the other hand, because overgrazing by cattle is common across the study area, we initially predicted a negative relationship between site occupancy and cattle incidence; however, our data did not support this prediction. Furthermore, previous studies have shown that distributions of prairie dogs and cattle may be positively associated, either because of cattle preferences to forage in prairie dog colonies or because prairie dogs select areas grazed by livestock (Knowles 1986, Detling 1998, Vermeire et al. 2004). We believe that the relatively homogeneous distribution of cattle across the entire study area likely obscured any relationship between prairie dog occurrence and cattle incidence.

Results of this study partially support predictions that prairie dogs living at the edge of geographical range would be highly selective in their use of habitat units and that average environmental conditions would differ from those of northern or central populations. We found evidence that prairie dogs of northwestern Chihuahua are selecting sites that differ markedly from most unused available areas. The relatively low probabilities of use estimated *a posteriori* for used locations suggest that availability of suitable locations is relatively low in the study area. The relatively high degree of habitat selectivity exhibited by prairie dogs in Chihuahua partially results from the high similarity in their habitat requirements compared to northern populations. However, it is evident that at least some of the prairie dog populations at the southern edge of their geographical range are more tolerant of variation in shrub density, forage cover, and soil type compared to populations in more northern regions. Our results highlight the importance of identifying the correct variables to be included in habitat suitability models for prairie dogs depending on the regional environmental context; otherwise, conservation and restoration efforts (e.g. reintroductions) could be done in suboptimal habitats.

MANAGEMENT IMPLICATIONS

In recent years, the grassland ecosystem of northwestern Chihuahua has been the focus of attention for an interdisciplinary group of agencies that includes the Mexican government, academic institutions, and NGOs, which are making efforts to decree the region that includes most of the area occupied by prairie dogs as a "Biosphere Reserve". In the face of economic pressures from farming, cattle ranching, and urban development, this group has started to plan management and conservation strategies to permit economic development in the future reserve without compromising the long-term persistence of the prairie dog ecosystem. However, at present, there is an urgent need for basic information about critical areas for prairie dog conservation and restoration, as well as the extent on which human activities may affect their distribution and abundance. Based on our results, we suggest that conservation efforts should be focused on areas that have short vegetation, preferably with low density of shrubs, and high herbage cover, in close proximity to other prairie dog colonies from which they are separated by relatively open habitat; these conditions could be created or promoted through habitat management to facilitate the expansion or recolonization of prairie dog towns. However, given the relatively high plasticity of these populations, we recommend the immediate protection of at least the largest colony found in savannah habitat to maintain genetic variability. Although our results show no significant effect of cattle ranching on prairie dog occurrence, more detailed, experimental studies are needed to better understand the relationships between prairie dogs and cattle. We contend that prairie dog populations living at the edge of the species' geographic range demand more attention not only because they have scarcer habitat (Proctor et al. 2006), but because population densities tend to be lower than in central regions (R. Avila-Flores unpublished data). Results of this study not only help to characterize critical habitats for prairie dogs in northwestern Chihuahua, but may help to identify suitable areas for conservation of species that largely depend on prairie dogs, such as burrowing owls (*Athene cunicularia*) and the recently reintroduced black-footed ferret (*Mustela nigripes*).

Table 3-1. Mean ($\bar{x}$), standard deviation (SD), and range of habitat variables measured at used and unused habitat units. We report statistical test results to illustrate the differences between used (n = 133) and unused (n = 151) habitat units, both for categorical (chi-square, χ^2) and continuous (t-values) variables. AB = Abbreviation of variable name.

		Unused habitat units			Used habitat units					
Variable	AB	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	t-value	χ^2	P
Soil type	ST	—	—	—	—	—	—	—	16.58	0.011
Soil texture-field	SF	—	—	—	—	—	—	—	7.82	0.098
Soil texture-map	SM	—	—	—	—	—	—	—	7.22	0.027
Soil moisture	M	—	—	—	—	—	—	—	2.27	0.321
Altitude (m)	A	1455.8	75.9	1339-1703	1445.9	50.3	1387-1652	1.27	—	0.207
Slope (degrees)	S	2.1	3.5	0-24	0.9	1.3	0-10	3.68	—	<0.001
Cattle dropping density (drop./ha)	C	423.0	555.6	0-2959	494.7	503.0	0-2296	-1.02	—	0.307
Shrub density (shrubs/ha)	SD	581.2	1036.0	0-8214	29.1	175.0	0-2092	10.15	—	<0.001
Shrub cover (%)	SC	6.9	10.6	0-47.2	0.3	1.5	0-10.6	8.67	—	<0.001
Herbage height (cm)	H	24.8	24.1	3-200	8.0	4.3	0-25	7.92	—	<0.001
Forbs cover (%)	F	15.4	15.1	0-100	13.6	7.9	0.2-35.0	0.60	—	0.550
Grass cover (%)	G	10.7	16.7	0-100	3.7	5.00	0-24.7	5.02	—	<0.001
Unpalatable veg. cover (%)	U	4.1	7.4	0-38.6	2.0	4.7	0-33.2	2.91	—	0.004
Dry vegetation cover (%)	D	3.4	5.5	0-49.0	2.4	2.9	0-16.9	1.57	—	0.119
Bare ground cover (%)	B	66.9	18.4	0-95.9	79.0	9.6	46.0-97.3	-6.60	—	<0.001
Colony area within 1 km (ha)	C1	20.1	47.9	0-206	100.9	88.9	0-314	-11.81	—	<0.001
Colony area within	C3	189.8	345.8	0-1537	514.5	484.1	0-1780	-8.51	—	<0.001

3 km (ha)										
Hostile area within 1 km (ha)	H1	137.5	138.3	0-524	80.0	105.2	0-314	3.81	---	<0.001
Hostile area within 3 km (ha)	H3	1174.4	871.4	0-2803	905.3	840.0	0-2827	2.32	---	0.021
Road density within 1 km (m)	R1	1080.5	1159.4	0-3921	980.4	1180.1	0-4412	0.68	---	0.500
Road density within 3 km (m)	R3	7120.5	5196.5	0-20480	7344.3	4972.7	0-19891	-1.22	---	0.224
Distance to main road (m)	DR	2727.9	2940.0	20-16273	2022.3	1852.3	22-9317	1.29	---	0.198
Distance to town (m)	DT	5527.2	4860.3	0-25995	4668.1	2915.9	40-11173	0.82	---	0.413

Table 3-2. Model performance statistics of global (G) and reduced (R) versions of 5 hypothetical models of habitat selection by black-tailed prairie dogs in northwestern Chihuahua. Statistics reported include number of parameters (*K*), deviance, Pseudo-R^2, second-order Akaike's Information Criterion (AIC_c), AIC_c differences (ΔAIC_c), and AIC_c weights (w_i). Abbreviations of variables are defined in Table 3-1.

Model	Variables in model	K	Deviance	Pseudo-R^2	AIC_c	ΔAIC_c	w_i
Biophysical-G	M+SM+ST+S+A+SD+H+F+G+D+U+B+C1	20	137.6	0.649	180.8	16.2	0.00
Biophysical-R	M+A+SD+H+F+G+D+U+B+C1	11	144.4	0.632	167.4	2.7	0.20
Vegetation-G	SD+H+F+G+D+U	7	171.6	0.563	186.0	21.4	0.00
Vegetation-R	SD+H+G+U	5	172.2	0.561	182.4	17.8	0.00
Visual obstruction	SD+H	3	184.2	0.531	190.3	25.6	0.00
Human impact-G	C+H1+R1+DR+DT	6	361.7	0.079	374.0	209.4	0.00
Human impact-R	H1+R1+DR+DT	5	362.7	0.076	372.9	208.3	0.00
Composite-G	M+A+SD+H+F+G+D+U+B+C1+H1+R1+DR+DT	15	139.7	0.644	171.5	6.9	0.02
Composite-R	M+A+SD+H+F+U+B+C1+H1	10	143.8	0.634	164.6	0.0	0.78

Table 3-3. Estimated coefficients, standard errors, odds ratios [exp (β)], Wald statistics and associated probabilities of habitat variables included in the top-ranking logistic model, after AIC model selection.

Habitat variable	β	SE	exp (β)	95% CI	Wald statistic	*P*
Soil moisture	1.186	0.587	3.27	1.04-10.36	4.08	0.044
Altitude	-0.015	0.005	0.98	0.98-0.99	10.73	0.001
Forb cover	0.064	0.037	1.07	0.99-1.15	3.09	0.079
Unpalatable veg. cover	0.155	0.045	1.17	1.07-1.28	11.79	0.001
Bare ground cover	0.056	0.037	1.06	0.98-1.14	2.27	0.132
Shrub density	-0.005	0.001	1.00	0.99-1.00	14.04	<0.001
Herbage height	-0.284	0.051	0.75	0.68-0.83	31.08	<0.001
Colony area within 1 km	0.009	0.004	1.01	1.00-1.02	5.95	0.015
Hostile area within 1 km	-0.003	0.002	1.00	0.99-1.00	2.67	0.102

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CHAPTER 4

SPATIAL VARIATION IN DEMOGRAPHIC INDICES OF BLACK-TAILED PRAIRIE DOGS: INFLUENCE OF LOCAL AND LANDSCAPE FACTORS

INTRODUCTION

All natural landscapes are patchy, to some extent and at some scale, in response to spatial variability in abiotic conditions, biotic interactions, and occurrence of random disturbances (Wiens 1976, Turner et al. 2001). Very often natural patchiness is increased by human activities which intensify disturbance levels and create new habitat patches (Turner et al. 2001). As a consequence of this environmental heterogeneity, habitat quality for populations and individuals varies over space. Because survival and reproduction of individuals vary with habitat quality (Van Horne 1983), local populations occupying different habitat patches often exhibit different demographic parameters and population dynamics (e.g. Wheatley et al. 2002, Lambrechts et al. 2004, Steenhof et al. 2006, Todd and Rothermel 2006). Indeed, small differences in resource distribution within the same habitat patch may generate different dynamics in adjacent subpopulations (Ehrlich 1965, Tavecchia et al. 2008). According to classical habitat-selection and population theories, high-quality habitats are more heavily used and support higher population growth rates and higher densities than low-quality habitats, but habitat quality is reduced as density approaches carrying capacity (Fretwell and Lucas 1969, Pulliam 1988). It has been noted, however, that strong selection and high population densities may not necessarily indicate high quality of habitats, as social dominance, migration patterns, and preference of low-quality areas may generate the opposite trend (Fretwell and Lucas 1970, Dwernychuk and Boag 1972, Van Horne 1983).

Resource availability and quality of local habitat are not the only factors driving demography and dynamics of populations. Theoretical and empirical developments in the fields of conservation biology, landscape ecology and metapopulation ecology have emphasized the roles of patch configuration (patch size and inter-patch distance) and spatial context (structure and nature of surrounding matrix) in the demography of spatially structured populations (Turner et al. 2001, Gaggiotti and Hanski 2004). According to the small-population paradigm of conservation biology (Caughley 1994), small populations (assumed to live in small habitat patches) face a higher risk of extinction compared to large populations because their growth rate is more sensitive to demographic, genetic, and environmental stochasticity (Shaffer 1981, Lande 1993, Reed 2004). Deterministic factors such as negative edge effects and Allee effects further contribute to reduce growth rates of small populations (Hokit and Branch 2003, Gaggiotti and Hanski 2004). However, theoretical relationships between population growth rate (or probability of persistence) and patch size do not help to predict population density based on patch size alone. Empirical analyses conducted on a variety of organisms have produced inconsistent relationships between density and patch size (Bowers and Matter 1997, Connor et al. 2000, Wilder and Meikle 2005), and different ecological theories (e.g. island biogeography, density compensation, or resource concentration hypotheses) either predict positive, negative, quadratic or null density-area relationships (Connor et al. 2000, Buckley and Roughgarden 2006).

Demography of local populations may be directly or indirectly influenced by patch isolation (Witt and Huntly 2001, Baguette and Schtickzelle 2006), which depends not only on the distance between patches but also on the suitability of the matrix habitat (Kotliar and Wiens 1990, Turner et al. 2001). Reduced immigration in highly isolated populations tends to lower their genetic diversity, which in turns contributes to reducing population fitness via inbreeding depression (Frankham 1998). It has been suggested that high dispersal rates in well-connected patches may rescue declining populations from extinction (Brown and Kodric-Brown 1977). Similarly, sink populations can only persist in the long term if they are well connected to source populations (Pulliam 1988). Inhospitable matrix habitat can produce an isolating "fence effect" in local populations, which results in reduced dispersal and increased population density (Krebs et al. 1969). In some cases, increased isolation can have positive effects in populations by reducing the movement of parasites and diseases (e.g. Johnson and Collinge 2004).

To better understand the processes driving the dynamics and demography of local populations, it is necessary to analyze the impact of factors operating at different spatial scales. However, because the quantification of precise demographic parameters and description of habitat metrics at multiple locations is a very difficult task (Skalski et al. 2005), relatively few studies have analyzed the combined effects of local habitat conditions and landscape structure on the demography and dynamics of local populations. Not surprisingly, such studies have found that local population dynamics is best explained by the interaction of some local and landscape factors (e.g. Verbeylen et al. 2003, Marchand and Litvaitis 2004, Dodd et al. 2006).

In this chapter, I used a correlative approach to analyze the impact of local and landscape factors on the demography of black-tailed prairie dogs (BTPDs) in a heterogeneous landscape of northwestern Chihuahua, Mexico. I examined short-term temporal changes both in BTPD demographic parameters and in local habitat factors as an additional approach to understand the effect of local processes. BTPDs are an appropriate model to analyze patterns of spatial variation in population performance because their populations are spatially structured as metapopulations (Lomolino and Smith 2001), they live in one of the most heterogeneous vegetation types (i.e. grasslands; Wiens 1976), and are relatively easy to count (e.g. Severson and Plumb 1998, Facka et al. 2008). The system of colonies of northwestern Chihuahua is particularly relevant because it constitutes one of the three largest BTPD complexes and includes the largest single colony in North America (Proctor et al. 2006). The study area is naturally heterogeneous, and is dominated by a mosaic of grasslands and shrublands which intermix at variable degrees (Ceballos et al. 2005, Chapter 2). Environmental heterogeneity is increased by anthropogenic disturbances, particularly by agriculture, urbanization and grazing by cattle (Ceballos et al. 2005, Chapter 2). Previous studies in other regions have found that demography (or persistence probability) of prairie dogs is influenced by resource quality and quantity (including positive edge effects; Garrett et al. 1982, Rayor 1985, Yeaton and Flores-Flores 2006, Facka et al. 2008), population size (Robinette et al. 1995), patch isolation, and spatial context of colonies (Lomolino and Smith 2001, Johnson and Collinge 2004, Magle et al. 2007, Chapter 2). Based on this knowledge, and considering that BTPD colonies in Chihuahua have been greatly fragmented (Chapter 2) and occupy one of the least-productive regions throughout the species' range (Facka et al. 2008, Avila-Flores et al. submitted), I expected a strong interactive impact of landscape configuration and forage availability on BTPD population performance.

METHODS

Study Area.—The system of BTPD colonies of northwestern Chihuahua, Mexico, is located 20-130 km south of the Mexico-U.S.A. border. In 2005, this colony complex consisted of at least 100 colonies (G. Ceballos and R. Avila-Flores unpublished data) scattered over a region of almost 400,000 ha (Marcé 2001). For simplicity, I considered all colonies within the study area as a single complex despite the fact that several of them are relatively (or completely) isolated. Colonies are located in a vast plain dominated by desert grasslands and shrublands (with interspersed patches of riparian, agricultural and small urban areas), bordered to the south and west by mountains of the Sierra Madre Occidental. Grassland vegetation is dominated by annual forbs, annual grasses, perennial grasses, and scattered shrubs (Desmond 2004). Climate is temperate arid with hot summers and cold winters, with a mean annual temperature of

15.7°C (range -15 – 50°C); mean annual precipitation is 307 mm, with most rains occurring from July to September and occasional snow showers in winter (García 1973). Agriculture and cattle ranching are prominent activities in the region. Recent declines in plant biomass and grass abundance, as well as increases in shrub encroachment and acceleration of erosion processes, have been considered consequences of overgrazing by cattle (Desmond 2004, Ceballos et al. 2005). However, it is likely that recent drought events enhanced the impact of cattle overgrazing (Chaper 2).

Demographic indices.— I established 45 160 x 160-m plots at 34 BTPD colonies distributed over the entire study area (Fig. 4-1), making an effort to maximize the range of local environmental conditions and the variety of spatial patterns within the plot sample. One plot was placed at each colony, except for the four largest colonies which had between 2 and 6 plots each. Plots were placed at accessible locations (often close to roads) at least 150-m from each other to maintain independence of sites (i.e. daily movements of each BTPD individual were restricted to only one plot). In 3 cases plots were smaller (100 x 100-m or 100 x 160 m) to fit dimensions of small colonies. I used large nails and colored rocks to permanently mark plot corners so that plot locations were exactly the same each year. Because both prairie dog density and local environmental conditions greatly varied over space even within the same colony, I constrained population inferences to the plot scale. Thus, for practical purposes, local populations or subpopulations in this chapter make reference to individual plots.

I estimated demographic indices for each plot based on visual counts of BTPDs (method adapted from Severson and Plumb 1998). Counts were conducted during two consecutive days in each plot between late-May and late-June 2005, 2006 and 2007, just after the first emergence of juveniles from burrows. Before starting counts, plot boundaries were delineated with colored flags. On a given count day, one observer arrived at the plot at around 0630 h which usually was prior to BTPD emergence. The observer sat 30-40 m from the eastern-most boundary of plot and did not begin observations for 30 min to habituate animals to his/her presence. BTPD individuals were counted with aid of binoculars (8 x 40 mm) by sweeping the plot at 15 min intervals between 0700 and 0900 h (period that includes the late-spring peak of activity; E. Rivera pers. comm.) and recording all visible adults and juveniles separately. I used the maximum aboveground count (MAGC), defined as the highest single count in two days, as an index of population density. Density was standardized by dividing the MAGC by the area of the plot. The MAGC is an appropriate population index when applied to large-scale studies (Facka et al. 2008) because of its simplicity and its moderate-to-high correlation with more robust and accurate density estimates (i.e. total censuses, mark-recapture, mark-resight; Severson and Plumb 1998, Magle et al. 2007, Facka et al. 2008). I did not apply any correction factor to MAGCs to account for differences in visibility between plots (as suggested by Severson and Plumb 1998), in order to avoid overestimation of BTPD density at suboptimal sites (i.e., sites with high vegetation or complex topography). Instead, counts at difficult plots were carefully conducted by the most experienced observer (R. Avila-Flores), and at the two most challenging plots two or three observers were used. Inter-observer variation in MAGCs, as measured by the average coefficient of variation (CV) from 8 independent assays (2-4 observers at each), was 0.072 (CV = 0.112 for adult counts; CV = 0.154 for juvenile counts). I used total (juveniles + adults) MAGCs to calculate the finite rate of population change between successive years (λ), which is appropriate for populations exhibiting annual pulses of birth (Eberhardt and Simmons 1992), using the formula $\lambda = MAGC_t/MAGC_{t+1}$. Annual productivity for each plot was estimated by the ratio of juveniles to adults, which is a metric that quantifies juvenile production as a function of the total breeding population (Skalski et al. 2005). To calculate this parameter, I divided the MAGC of juveniles by the MAGC of adults for a given year.

Local habitat variables.— At each sampling plot, I measured habitat variables that reflect important features for BTPDs (e.g. Avila-Flores et al. submitted), including food availability, magnitude of visual obstruction, abundance of large herbivore competitors, abundance of predators and soil properties. Herbage cover was sampled twice a year in 2005 and 2006, once during the dry season (late-May to late-June) and once during the peak of the rain season (late-July to late-August); in 2007 it was sampled only during the dry season. Partial herbage cover data (n = 25 plots) were collected during the rain season 2004. I visually estimated the percent cover of grasses, forbs, unpalatable forage (spiny, sticky or woody plants; e.g. *Amaranthus palmeri*, *Gutierrezia sarothrae*, *Salsola kali*, *Solanum eleagnifolium*) and dry (standing-dead) vegetation within square frames of 50 × 50 cm (with strings attached at 5-cm intervals to form a grid of 100 small squares) that were systematically placed in a grid of 7 x 7 spaced at 20-m intervals (n = 49; in the case of the 3 small plots, n = 28 or 16), with first lines and rows being 20 m inwards from plot boundaries; the average percent cover was used for statistical analyses. I used the same square frames (n = 49, 28 or 16) to visually estimate the average height of the herbage stratum (in cm) during the dry seasons 2006 and 2007 and the rainy season 2006. I measured the dominant dimensions of every shrub (length, width and height in cm) whose stem fell within the 160 x 160-m plot to calculate an index of visual obstruction by shrubs. I assumed a regular hexahedral shape of each shrub to calculate its volume, and weighted that value by its relative canopy density (0.33 = low density, for shrubs with scarce or no leaves; 0.66 = medium density, for shrubs whose canopy allows some visibility from the BTPD standpoint; 1.0 = high density, for shrubs whose dense canopy makes it difficult or impossible to look through). The index of shrub obstruction was then calculated by summing the weighted volumes of all shrubs within the plot, standardizing this value per unit area (ha) to account for differences in plot size. Relative activity of large herbivores within the plot was estimated by counting the number of cattle and horse droppings within 7 strip-transects (160 x 2 m) spaced at 20-m intervals, and then expressing this value as dropping density per hectare. Hereafter, herbivore dropping density will be referred to as cattle dropping density considering the dominance of beef cattle. Relative abundance of predators was estimated by the cumulative number of potential predators (within 200 m of the plot center) observed during the above ground counts of BTPD. This included coyotes (*Canis latrans*), domestic dogs (*Canis lupus familiaris*), bobcats (*Lynx rufus*), badgers (*Taxidea taxus*) and raptors (Falconiformes). The index of shrub obstruction, cattle activity, and predator abundance were estimated once a year at the time of BTPD counts. Biological attributes of each plot measured at different years are shown in Appendix VI.

Soil properties were measured only once from samples collected in July 2007. I used a shovel to collect one soil sample (20-cm in diameter, 20-cm deep) at each of 4 quadrants within each plot. The four samples were mixed in a bucket, and a small sample of this mixture was taken to the lab. Real soil density, apparent soil density, pH, as well as percent content of organic matter, sand, loam and clay, were measured at the Laboratory of Edaphology, FES-Iztacala UNAM (Tlalnepantla, Mexico), using standard methods (Muñoz Iniestra et al. 2006). Soil properties of each plot are shown in Appendix VII.

Landscape variables.—I used GIS and remote sensing techniques to infer the population effects of patch configuration (colony size and isolation), spatial context (particularly the proportion of hostile habitat in the surroundings), proximity to edge habitat, and incidence of human features. Colony maps were generated based on GPS readings taken in 2005 at boundaries of all colonies known at that time (most data provided by G. Ceballos and colleagues). Areas of use (polygons) separated by < 100 m were considered as a single colony. Land cover maps were created using Landsat-GLS scenes from 2005, which were classified based on decision-tree algorithms in programs ENVI and ERDAS (see

Chapter 2 for details). Colony size was measured as the area of the colony within which the plot was located. Degree of isolation (a parameter negatively related to the number of potential immigrants) was measured in two ways: by the number of BTPD colonies within circular buffers of 1- and 3-km of radius from plot centers, and by the area covered by BTPD colonies within the same buffer areas. To describe landscape-scale habitat, I measured the area covered by shrublands, agricultural lands, and hostile habitat (the sum of area covered by water bodies, shrublands, woodlands, agricultural lands, and urban areas) within 1- and 3-km circular buffers. Proximity to edge habitat was measured as the linear distance between plot centers and the nearest colony edge. Incidence of human features was measured by two parameters: by the linear distance of plot centers to nearest town, and by the linear distance to nearest main road (the road map was obtained on-line from the website of *Comisión Nacional para el Conocimiento y Uso de la Biodiversidad*, CONABIO, Mexico). All spatial analyses were performed in ArcGIS 9.1. Landscape attributes of each plot are presented in Appendix VII.

Statistical analyses.—I fitted generalized linear mixed-effects models (GLMMs) of Gaussian family and log link functions to identify the local and landscape factors that best explain differences in demographic indices (relative density, ratio of juveniles to adults, and rate of population change) among BTPD subpopulations. I defined "year" and "plot" as random variables in the GLMMs to account for correlation of data; all local and landscape factors were defined as fixed variables. Using the entire 3-year data set I built 4 models for each demographic index, each model representing a different hypothesis: 1) landscape model, 2) local habitat model, 3) soil properties model, and 4) combined model (using a combination of variables from previous models). I separated soil properties from other local habitat variables to reduce the number of parameters in models. The only explanatory variables that changed over time in models were local habitat variables, whereas landscape and soil variables were assumed to remain static during the course of this study. In order to be biologically relevant, habitat models for a given year (t) included herbage cover and height from that same-year (t) dry season (which reflects food availability by the end of the breeding season) as well as herbage cover and height from previous-year (t-1) rainy season (which reflects the annual peak of food availability, ~6-7 months before the birth season). For modeling the rate of population change, I included an additional local habitat model (2a) expressing environmental variables (x) as finite rates of change (R) from one dry season to next (to correspond with timing of BTPD rates of change) of the form $R = x_t/x_{t+1}$, which is equivalent to the population rate of change used for BTPDs. When a pair of explanatory variables was redundant (e.g. those variables that measure the same landscape attribute at different scales), I selected the single variable that reduced residual deviance the most when included with the rest of variables. Because some explanatory variables might exhibit non-linear relationships with demographic parameters (e.g. incidence of cattle or colony size), I tested the influence of some quadratic terms in global model performance.

I produced two types of models to represent each of the 4 hypotheses previously described, one global model that included all variables and one more parsimonious model obtained through best subsets techniques (after removal of highly correlated variables; see Appendix VIII). The global model is reported to illustrate the maximum explanatory power of each hypothesis given the data and the variables included, having in mind the risk of overfitting. Variables in the global model of hypothesis 4 (combined model) were selected based on best subsets of models 1-3. I selected the best subset of variables from each global model based on the Akaike's Information Criterion for small sample sizes (AIC_c), removing at each step the variable whose exclusion minimized the AIC_c value; this process was repeated until no additional deletion improved performance of the more parameterized preceding model. Overall, I obtained a set of 8 candidate models (10 in the case of rate of population change) to describe each demographic index. I selected the model that best explained each demographic index based on information-theoretic methods. AIC_c, ΔAIC_c, and AIC weight (w_i) were used to rank competing models (Burnham and Anderson 2002). The model chosen as the best, given our data, was that model with the lowest AIC_c and highest w_i values, provided that no other model had a ΔAIC_c close to 2.

I produced separate sets of generalized linear models (Gaussian family and log link function) for years 2005, 2006 and 2007 in order to know how habitat associations of BTPD density and juvenile-to-adult ratio change over time. Similarly, I produced separate model sets for periods 2005-2006 and 2006-2007 to explain spatio-temporal differences in rate of population change. I used the procedure and techniques described in previous paragraphs to build year-specific models. However, considering that local habitat variables were the only ones that changed over time along with demographic indices, I fitted year-specific models only using local habitat variables (hypothesis 2); dry-season habitat variables included in these models were expressed as rates of change. Information-theoretic methods were used to identify the most influential habitat variables. I report deviance and pseudo-R^2 to provide additional measures of model fit (Hoffman 2004). All statistical analyses were performed in S-Plus and R.

RESULTS

Spatial variation in demographic parameters.—Overall, modeling exercises suggested that demography of BTPDs is more influenced by local (biotic) habitat conditions and their temporal variability than by landscape configuration or soil properties. Although generalized linear mixed-effects models (GLMMs) showed that landscape, local and soil variables had a similar explanatory power to explain differences in demographic indices, the impact of local conditions was most likely minimized in models because much of their spatio-temporal variation was captured in the random terms (year and plot). Furthermore, local habitat variables were sufficient to explain a relatively high proportion of variability in demographic parameters (particularly in relative density) within a given year (Tables 4-1, 4-2 and 4--3). In general, my models show that sites with low forage production (cover and height) during the rain season and high forage cover during the dry season in medium-sized colonies tend to support higher densities, higher juvenile production levels, and higher rates of population change of BTPDs. In contrast, as explained below, the association between demographic indices and most landscape and soil variables was less consistent.

Spatial variation in relative density (MAGC) during the 3-year study was best modeled by a combination of landscape and local factors after accounting for the autocorrelative effects of plot and year (Tables 4-1 and 4-4). In the best GLMM, most variance was associated to differences between plots (62%) and between years (14%); therefore, spatial models dealt with only 24% of (residual) variance. Based on values of deviance and *Cp* scores, the most influential factors explaining differences in density among subpopulations were (in parenthesis the sign of the relationship; Table 4-4) colony size (negative quadratic; Fig. 4-2), number of colonies within 1 km (negative), cattle activity (negative quadratic), cover of unpalatable forage during both dry (negative; Fig. 4-2) and rainy (positive) seasons, soil density (positive), soil organic matter (negative) and soil pH (negative). Year-specific habitat models for 2005, 2006 and 2007 suggest that BTPDs exhibit higher densities at sites with low herbage production during the previous-year rain season and high cover of grasses/forbs during the current-year dry season (Fig. 4-2). Grass cover during the previous-year rainy season had a positive effect on juvenile production only in 2006, which was a year with very low winter-spring plant production. Positive relationships with cattle (quadratic) and shrubs became evident when data were analyzed on a year-specific basis (Table 4-1). The only variable that consistently appeared in all reduced models (with negative effect) was the cover of unpalatable forage during the dry season (Table 4-4).

Variation in the ratio of juveniles to adults using the 3-year dataset was best explained by a combination of local and landscape factors once the effects of plot and year were controlled (Table 4-2). In this model, a relatively high proportion of variance (40%) was explained by differences in juvenile production between years. The strong influence of the random variable "year" was largely due to the generalized reproductive crash that occurred in 2006, when most subpopulations failed to reproduce and variance between sites was almost zero. After accounting for random variables, it was observed that more juveniles are produced on sites with either low or high cattle activity and less dense soils in medium-sized colonies (Table 4-5; Fig. 4-3). Although this model does not include vegetation variables, year-specific models illustrate the relative importance of vegetation attributes for juvenile production in BTPDs. In 2005 and 2006, cover of grasses/forbs during the dry season was a positive predictor of juvenile production (Fig. 4-3); in contrast, cover of unpalatable vegetation during the same season was negatively related with juvenile production. In the same models, cover of forbs/grasses during the previous-year rainy season was negatively related with this demographic parameter (Table 4-5; Fig. 4-3). As in density models, cattle activity (quadratic term) and shrub cover appeared as positive covariates of juvenile production (Tables 4-2 and 4-5).

Models including both local and landscape variables were best to explain spatial differences in rate of BTPD population change during the periods 2005-2006 and 2006-2007 (Table 4-3). However, a high proportion of variance (39%) was explained by differences in rate of population change between periods (during the period 2005-2006 most populations declined, whereas during 2006-2007 most of them grew). According to the best model, increases in cover of dry vegetation from one dry season to the next promote an increase in prairie dog numbers (Fig. 4-4). These models also suggest that colony size (quadratic relationship; Fig. 4-4) and soil density are negatively related to the annual rate of BTPD population change (Table 4-3). The most parsimonious model for period 2006-2007 confirms the relatively strong association between the rate of BTPD population change and changes in cover of dry forage (positive relationship) and unpalatable forage (negative relationship; Fig. 4-4) during the rain season (Table 4-3). The height of herbage layer during the dry season was one of the most important factors explaining changes in BTPD population numbers during the period 2005-2006 (Table 4-3; Fig. 4-4). Interestingly, the height of the herbage layer during the dry season had a positive effect during a period of low spring plant productivity (2005-2006) but a negative effect during a period of high spring plant productivity (2006-2007).

Temporal variation in demographic parameters.—Numbers of BTPDs greatly changed during the 3-year study. The most remarkable pattern was the generalized population decline in 2006 (Fig. 4-5a), when reproduction at most subpopulations was totally suppressed (Fig. 4-5b). By 2007, 28 subpopulations were recovering after the 2006 decline, 7 were still declining, 6 became locally extinct and 3 kept numbers relatively stable; only 1 subpopulation exhibited a slight but sustained growth from 2005 to 2007. Variation in population density between years was higher than variation in density among sites within a given year ($\text{ANOVA}_{44,2}$, $F = 5.75$, $P < 0.001$), which indicates a high degree of spatial synchronization in population dynamics during the period of study. Interestingly, changes in BTPD population numbers and reproduction closely resemble the changes in herbage cover during the dry season (Fig. 4-5c), but they contrast with the change in herbage cover during the (previous-year) rainy season which exhibits an increasing trend over time (Fig. 4-5d). No other biotic factor resembles the pattern of temporal change of BTPD density or reproduction.

DISCUSSION

This study constitutes the first attempt to simultaneously evaluate and compare the relative impacts of local and landscape factors on BTPD population performance. Because BTPDs in southwestern U. S. and northwestern Mexico are faced with the driest conditions within the species' geographic range (Facka et al. 2008, Avila-Flores et al. submitted), I expected forage production to be one of the most limiting factors for BTPD populations in northwestern Chihuahua. In support of this prediction, I found that demographic parameters of Chihuahuan BTPD populations respond more to local environmental conditions, particularly forage production, than to large-scale landscape factors. However, as discussed below, population responses to local habitat conditions are not simple and vary over time.

Results of this study suggest that either high or low extremes in forage production may have negative impacts on BTPD populations. On one hand, the population benefits of living on highly productive sites result counterintuitive as BTPDs depend on grasses and forbs as their main source of food (Hoogland 1995). Indeed, available information on the demography of black-tailed, Gunnison's and Mexican prairie dogs indicates that populations living on sites with higher forage production exhibit higher levels of density, fecundity, survivorship, average body size and/or juvenile growth (Garrett et al. 1982, Rayor 1985, Rioja 2003, Yeaton and Flores-Flores 2006). It is likely that BTPD populations living at the driest portions of the species' range are particularly sensitive to spatial and temporal differences in forage production. For example, in central Mexico (southern Coahuila and northern San Luis Potosí), density of Mexican prairie dogs (a closely-related species that lives in habitats similar to those of southern BTPDs) was 3.5 times greater and plant biomass 7 times higher on a site with alluvial soil as compared to a site with gypsum-derived soil (Yeaton and Flores-Flores 2006). In central New Mexico, a sharp decline in BTPD population density in 2004 coincided with a period of below-average precipitation in 2003, which likely caused a strong reduction in plant productivity (Facka et al. 2008). Results of this study go beyond and suggest that density, juvenile production and rate of population change of BTPDs are strongly influenced by forage availability during the driest part of the year. The fact that the rate of change in standing-dead vegetation cover during the late dry season (mid-May to mid-June) was positively related to the rate of BTPD population change suggests that I may have failed to record vegetation in the most critical period for BTPDs. Such critical period might correspond to the BTPD reproductive season (the period from mating to juvenile weaning), which in northern Mexico seems to occur between late February and mid-May. Reduced moisture levels observed during the winter 2005-2006, when no snow showers occurred and frost events were scarce (as stated by local residents), could therefore explain the striking reduction in forage cover as well as the reduced population performance (especially the failure to reproduce) of BTPDs measured during the spring 2006.

Paradoxically, high levels of forage production resulting from summer rain events seem to affect negatively performance of BTPD populations. This interpretation is supported by the fact that the cover (or height) of forage during the rainy season of the preceding year was negatively related with all demographic indices. Although contradictory, this result may be explained in the light of basic knowledge of BTPD biology. It is well-known that BTPDs actively select sites with short vegetation in order to facilitate detection of predators (Knowles 1986, Cincotta et al. 1987, Hoogland 1995, Milne-Laux and Sweitzer 2006, Terrall 2006, Augustine et al. 2007, Avila-Flores et al submitted), and that, pursuing the same goal, BTPDs constantly clip vegetation to keep it short (Hoogland 1995, Weltzin et al. 1997). When rain events are short and intense (as those occurring in the Chihuahuan Desert), BTPDs may be unable to keep vegetation short and are forced to move to neighboring areas; alternatively, BTPDs die as a consequence of increased predation.

Soil properties are considered important features of BTPD habitat as they affect the ability of individuals to dig as well as the stability of burrows systems (Clippinger 1989, Roe and Roe 2003). In addition, soil characteristics influence the level of plant productivity in prairie dog habitats (Yeaton and Flores-Flores 2006). Although BTPDs may occupy any well-drained soil that can support their burrow systems, they seem to avoid soils with high content of sand and rocks (Reading and Matchett 1997, Roe and Roe 2003). In this study, however, I found inconsistent effects of soil properties on BTPD demographic parameters. Soil density, a factor related with porosity and drainage ability, was present at best BTPD demographic models. However, the influence of this factor on BTPD demography was inconclusive, as denser soils were associated to high population densities but also to low juvenile productions and low rates of populations change.

Recent declines in BTPD populations in Mexico have been partially explained by habitat quality reductions caused by livestock overgrazing and shrub encroachment (Marcé 2001, Ceballos et al. 2005). Based on these hypotheses, I predicted negative impacts of intense cattle activity and shrub cover indices on the demography of BTPDs. However, my results do not support these predictions. Although cattle activity is present at most parsimonious models, its relationship with demographic parameters is quite inconsistent. Whereas some models indicate positive quadratic relationships between cattle activity and demographic indices, others indicate negative quadratic relationships. Therefore, it is likely that the observed quadratic relationships are just an artifact resulting from few outlier locations. In any case, my results do not provide clear evidence that heavy grazing by cattle has a negative impact on BTPD populations (at least during years with close-to-average precipitation). On the other hand, my results suggest that BTPD subpopulations living in savannah habitat exhibit some of the highest densities and juvenile productions. These results might be indicative of real advantages of living on sites with high cover of shrubs, as shown for other ground squirrels (Hannon et al. 2006) and as suggested by personal unpublished behavioral data, or they may result from the fact that savannah sites also exhibited high levels of forage cover in late spring.

Available information suggests that landscape structure may have important impacts on BTPD populations. In theory, BTPDs should benefit from large colony sizes as survival rates increase with population size (Robinette et al. 1995). In agreement with that prediction, Lomolino and Smith (2001) and Lomolino et al. (2003) observed that large colonies in Oklahoma had a higher probability of persistence during the periods 1967-1989 and 1989-1997 than small colonies. However, my results failed to demonstrate any demographic benefit of living in large colonies for BTPDs. Although small colonies tended to exhibit low population densities, low juvenile productivities and small rates of population change, the opposite trend did not hold for large colonies of BTPDs. The low performance of subpopulations in the largest colony likely resulted from particular environmental conditions at the local scale, as these grasslands apparently developed on eroded, low-productivity sandy soils.

The impact of colony isolation on performance of BTPD populations seems to be context-dependent. For example, increased isolation of colonies may reduce their risk of extinction in regions affected by plague (Lomolino and Smith 2001, Lomolino et al 2003), but the extinction risk may increase in isolated colonies in arid regions in response to small differences in forage production (Scott-Morales et al. 2005, Chapter 1). In this study, isolation of colonies (as measured by the number of neighbor colonies) explained a small proportion of variance in population density. However, and contrary to my original predictions, isolation had a positive effect on demographic parameters. In other words, subpopulations that were surrounded by a high proportion of hostile habitat or were closer to human features exhibited higher densities. Although unexpected, these results are similar to those of recent studies which have recorded the highest BTPD densities at colonies surrounded by urban areas and roads (Johnson and Collinge 2004, Magle et al. 2007). Because hostile areas around colonies may serve as effective dispersal barriers for BTPDs, high densities at such places can be explained by the "fence effect" described by Krebs et al. (1969). However, it is less clear why these isolated populations tend to produce more juveniles.

It was interesting that two subpopulations occupying highly-disturbed habitats exhibited relative densities and juvenile productions much higher than the rest of sites. Both sites were located at small colonies (<10 ha), were very close to human settlements (distance < 150 m), were mostly surrounded by shrublands and/or agricultural lands, and were sparsely covered by vegetation during the dry season. One of these sites was partially used as a farmyard to stock cattle and the other was sometimes used as a baseball field within a ranch. These observations are intriguing as hostile encounters of BTPDs with humans increase their stress levels and reduce reproductive success (Vosburgh and Irby 1998, Pauli and Buskirk 2007). The key to understand these striking results may be given by other demographic or life-history parameters not measured in this study. For example, it is likely that survival rates in these subpopulations were lower than in other places; in fact, posterior trappings at these locations revealed that many of the resident BTPDs exhibited high ectoparasite loads and were in poor body condition. As discussed above, I could have failed to measure forage availability at the most critical period for these subpopulations. Factors not considered in this study, such a food quality and plant community composition, may help to explain such extreme situations. Long-term studies coupling more precise demographic data with detailed habitat descriptions are needed to better understand responses of BTPDs to different landscape structures and to climatically-driven environmental changes.

Table 4-1. Global (G) and reduced (R) versions of generalized linear mixed-effects models representing 4 competing hypotheses that explain spatial variation in relative density of BTPDs. Year-specific generalized linear models only represent the habitat hypothesis. Different measures of model performance based on residual deviance are reported. Abbreviations of explanatory variables are: CS = colony size, NC1 = number of colonies within 1 km, AC1 = area covered by BTPD colonies within 1 km, AH1 = area covered by hostile habitat within 1 km, DE = distance to edge, DR = distance to road, DT = distance to town, Ct = cattle activity, Pr = incidence of predators, Sh = shrub obstruction index, HHD and HHR = herbage height in dry and rain seasons, DVD and DVR = dry vegetation cover in dry and rain seasons, UVD and UVR = unpalatable vegetation cover in dry and rain seasons, FbD and FbR = forbs cover in dry and rain seasons, GsD and GsR = grass cover in dry and rain seasons, SD = soil density, Cl = soil clay content, Sa = soil sand content, OM = soil organic mater, pH = soil pH.

Model	Variables	K	Deviance	AIC$_c$	ΔAIC$_c$	w_i	Pseudo-R^2
All data							
Landscape-G	CS+CS^2+NC1+AC1+AH1+DE+DR+DT	12	740.6	767.7	67.7	0.00	
Landscape-R	CS+ CS^2+NC1	7	702.8	717.9	17.9	0.00	
Habitat-G	Ct+Ct^2+Pr+Sh+DVD+UVD+FbD+GsD+DVR+UVR+FbR+GsR	16	711.8	749.5	49.5	0.00	
Habitat-R	Ct+Ct^2+UVD+FbD+UVR	9	698.9	718.7	18.7	0.00	
Soil-G	SD+Sa+Cl+OM+pH	9	707.5	727.3	27.3	0.00	
Soil-R	SD+OM+pH	7	705.8	720.9	20.9	0.00	
Combined-G	CS+CS^2+NC1+Ct+Ct^2+UVR+UVD+FbD+SD+OM+pH	15	666.2	701.2	1.2	0.36	
Combined-R	CS+CS^2+NC1+Ct+Ct^2+UVR+UVD+	14	667.7	700.0	0.0	0.64	

	SD+OM+pH						
2005							
Habitat-G	Ct+Ct^2+Pr+Sh+DVD+UVD+FbD+ GsD+DVR+UVR+FbR+GsR	13	197.9	264.4	8.1	0.02	0.524
Habitat-R	Ct+Ct^2+Sh+UVD+GsD+UVR+FbR	8	230.0	256.3	0.0	0.98	0.447
2006							
Habitat-G	Ct+Ct^2+Pr+Sh+HHD+DVD+UVD+ FbD+GsD+DVR+UVR+FbR+GsR	14	149.4	191.4	11.4	0.00	0.808
Habitat-R	Ct+Ct^2+Sh+UVD+FbD+DVR+UVR+GsR	9	156.8	180.0	0.0	1.00	0.798
2007							
Habitat-G	Ct+Ct^2+Pr+Sh+HHD+DVD+UVD+ FbD+GsD+HHR+DVR+UVR+FbR+GsR	15	1618.7	1665.2	0.0	0.72	0.570
Habitat-R	Ct+Ct^2+Pr+HHD+DVD+UVD+FbD+ GsD+HHR+DVR+UVR+FbR+GsR	14	1625.2	1667.2	1.9	0.28	0.569

Table 4-2. Global (G) and reduced (R) versions of generalized linear mixed-effects models representing 4 competing hypotheses that explain differences in juvenile production of BTPDs. Year-specific generalized linear models only represent the habitat hypothesis. Different measures of model performance based on residual deviance are reported. See Table 4-1 for meaning of variable abbreviations.

Model	Variables	K	Deviance	AIC$_c$	ΔAIC$_c$	w_i	Pseudo-R^2
All data							
Landscape-G	CS+CS^2+NC1+AC1+AH1+DE+DR+DT	12	428.1	455.2	79.0	0.00	
Landscape-R	CS+CS^2	6	365.4	378.2	1.9	0.22	
Habitat-G	Ct+Ct^2+Pr+Sh+DVD+UVD+FbD+GsD+DVR+UVR+FbR+GsR	16	415.0	452.7	76.4	0.00	
Habitat-R	Ct+Ct^2+FbD	7	367.8	382.9	6.6	0.02	
Soil-G	SD+Sa+Cl+OM+pH	9	379.0	398.7	22.5	0.00	
Soil-R	SD+OM	6	367.9	380.7	4.4	0.06	
Combined-G	CS+CS^2+ Ct+Ct^2+FbD+SD+OM	11	354.7	379.3	3.1	0.12	
Combined-R	CS+CS^2+ Ct+Ct^2+SD	9	356.5	376.2	0.0	0.58	
2005							
Habitat-G	Ct+Ct^2+Pr+Sh+DVD+UVD+FbD+GsD+DVR+UVR+FbR+GsR	13	44.4	110.9	41.0	0.00	0.369
Habitat-R	Sh+UVD+GsD+FbR+GsR	6	52.6	69.9	0.0	1.00	0.252
2006							
Habitat-G	Ct+Ct^2+Pr+Sh+HHD+DVD+UVD+FbD+GsD+DVR+UVR+FbR+GsR	14	1.1	43.1	32.8	0.00	0.378
Habitat-R	UVD+FbD+GsR	4	1.3	10.3	0.0	1.00	0.261
2007							
Habitat-G	Ct+Ct^2+Pr+Sh+HHD+DVD+UVD+FbD+GsD+HHR+DVR+UVR+FbR+GsR	15	63.4	110.0	25.6	0.00	0.320
Habitat-R	Ct+Ct^2+FbD	4	75.4	84.4	0.0	1.00	0.192

Table 4-3. Global (G) and reduced (R) versions of generalized mixed-effects models representing 5 competing hypotheses that explain spatial variation in the rate of population change of BTPDs. Separate generalized linear models for periods 2005-2006 and 2006-2007 only represent the habitat hypothesis. Several measures of model performance based on residual deviance are reported. See Table 4-1 for meaning of variable abbreviations. Variables followed by (R) indicate that they are expressed as rates of change from one year to the next.

Model	Variables	K	Deviance	AIC$_c$	ΔAIC$_c$	w_i	Pseudo-R^2
All data							
Landscape-G	CS+CS^2+NC1+AC1+AH1+DE+DR+DT	12	321.3	349.4	82.3	0.00	
Landscape-R	CS+CS^2	6	254.6	267.6	0.5	0.25	
Habitat-G	Ct+Ct^2+Pr+Sh+HHD+DVD+UVD+FbD+GsD+ DVR+UVR+FbR+GsR	17	301.1	343.7	76.6	0.00	
Habitat-R	Ct+Ct^2	6	256.7	269.7	2.6	0.09	
Habitat change-G	Ct(R)+Sh(R)+DVD(R)+UVD(R)+FbD(R)+GsD(R)	10	284.4	307.2	40.1	0.00	
Habitat change-R	DVD(R)+UVD(R)	6	257.5	270.5	3.4	0.06	
Soil-G	SD+Sa+Cl+OM+pH	9	269.2	289.5	22.4	0.00	
Soil-R	SD	5	258.6	269.3	2.2	0.11	
Combined-G	CS+CS^2+ Ct+Ct^2+DVD(R)+UVD(R)+SD	11	243.1	268.5	1.4	0.16	
Combined-R	CS+CS^2+ Ct+Ct^2+DVD(R)+SD	10	244.3	267.1	0.0	0.33	
2005-2006							
Habitat-G	Ct(R)+Sh(R)+HHD+DVD(R)+UVD(R)+FbD(R)+ GsD(R)+DVR+UVR+FbR+GsR	12	4.4	59.6	44.5	0.00	0.353
Habitat-R	HHD+UVR+FbR	4	4.9	15.1	0.0	1.00	0.290
2006-2007							
Habitat-G	Ct(R)+Sh(R)+HHD+DVD(R)+UVD(R)+FbD(R)+ GsD(R)+HHR+DVR+UVR+FbR+GsR	13	61.1	99.2	21.6	0.00	0.275
Habitat-R	DVD(R)+UVD(R)	3	71.0	77.6	0.0	1.00	0.158

Table 4-4. Variables included in best models (after AIC model selection) that explain total and year-specific differences in relative density of black-tailed prairie dogs in northwestern Chihuahua. Estimated coefficients, standard errors and associated *t*-values are reported.

Variable	β	SE	*t*-value
All data			
Colony size	-10.641	12.990	-0.82
Colony size^2	-14.035	11.563	-1.21
Number of colonies within 1 km	-0.503	1.375	-0.37
Cattle dropping density	-1.087	7.198	-0.15
Cattle dropping density^2	-5.104	6.236	-0.82
Unpalatable vegetation cover (rainy)	0.173	0.073	2.38
Unpalatable vegetation cover (dry)	-0.687	0.209	-3.29
Soil density	2.450	16.405	0.15
Soil organic matter	-1.979	3.158	-0.63
Soil pH	-0.784	1.831	-0.43
2005			
Cattle dropping density	-3.860	6.638	-0.58
Cattle dropping density^2	-3.059	7.184	-0.43
Shrub obstruction index	0.015	0.013	1.13
Unpalatable vegetation cover (rainy)	-3.874	5.397	-0.72
Forb cover (rainy)	-0.143	0.088	-1.62

Unpalatable vegetation cover (dry)	-1.460	0.568	-2.57
Grass cover (dry)	0.005	0.317	0.02
2006			
Cattle dropping density	1.684	2.206	0.76
Cattle dropping density^2	8.184	2.318	3.53
Shrub obstruction index	0.004	0.002	1.76
Dry vegetation cover (rainy)	-0.588	0.275	-2.14
Unpalatable vegetation cover (rainy)	0.125	0.044	2.86
Grass cover (rain)	0.107	0.039	2.72
Unpalatable vegetation cover (dry)	-1.114	0.188	-5.93
Forb cover (dry)	3.058	0.309	9.91
2007			
Cattle dropping density	24.180	14.182	1.70
Cattle dropping density^2	31.296	9.843	3.18
Predator abundance	-2.042	1.567	-1.30
Herbage height (rainy)	-0.643	0.448	-1.44
Dry vegetation cover (rainy)	2.162	3.455	0.63
Unpalatable vegetation cover (rainy)	-0.618	0.413	-1.50
Forb cover (rainy)	-0.520	0.158	-3.29
Grass cover (rainy)	-0.089	0.197	-0.45
Herbage height (dry)	-1.630	0.950	-1.72
Dry vegetation (dry)	0.338	0.166	2.04
Unpalatable vegetation cover (dry)	-0.678	0.422	-1.61

Forb cover (dry)	1.249	0.534	2.34
Grass cover (dry)	1.068	1.222	0.87

Table 4-5. Variables included in best models (after AIC model selection) that explain total and year-specific differences in juvenile production of black-tailed prairie dogs in northwestern Chihuahua. Estimated coefficients, standard errors and associated *t*-values are reported.

Variable	β	SE	*t*-value
All data			
Colony size	-1.613	1.284	-1.26
Colony size^2	-1.625	1.267	-1.28
Cattle dropping density	0.968	1.288	0.75
Cattle dropping density^2	0.539	1.260	0.43
Soil density	-1.317	1.476	-0.89
2005			
Shrub obstruction index	0.005	0.003	1.54
Forb cover (rainy)	-0.059	0.037	-1.59
Grass cover (rainy)	-0.100	0.076	-1.32
Grass cover (dry)	0.236	0.209	1.13
Unpalatable vegetation cover (dry)	-0.307	0.235	-1.31
2006			
Grass cover (rainy)	-0.007	0.003	-2.08
Unpalatable vegetation cover (dry)	-0.023	0.013	-1.87
Forb cover (dry)	0.072	0.025	2.94
2007			

Cattle dropping density	1.193	1.356	0.88
Cattle dropping density^2	2.728	1.368	1.99
Forb cover (dry)	-0.179	0.072	-2.47

Table 4-6. Variables included in best models (after AIC model selection) that explain total and period-specific differences in rate of population change of black-tailed prairie dogs in northwestern Chihuahua. Estimated coefficients, standard errors and associated *t*-values are reported.

Variable	β	SE	*t*-value
All data			
Colony size	-0.161	1.126	-0.14
Colony size^2	-1.261	1.095	-1.15
Cattle dropping density	-0.765	1.118	-0.68
Cattle dropping density^2	1.067	1.058	1.01
Change in dry vegetation cover (dry)	0.113	0.040	2.84
Soil density	-1.205	1.519	-0.79
2005-2006			
Unpalatable vegetation cover (rainy)	-0.013	0.007	-1.80
Forb cover (rainy)	-0.012	0.006	-2.09
Herbage height (dry)	0.031	0.008	3.79
2006-2007			
Change in dry vegetation cover (dry)	0.109	0.054	2.01
Change in unpalatable vegetation cover (dry)	-0.072	0.037	-1.98

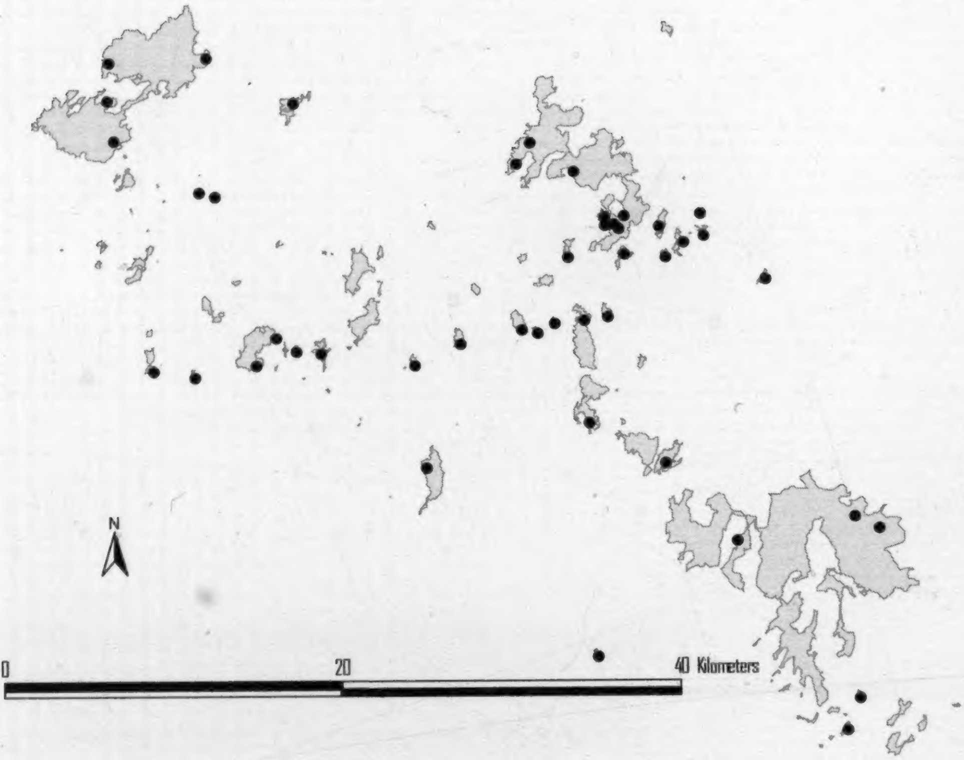
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Fig. 4-1. Distribution of sampling plots in the complex of black-tailed prairie dog colonies in northwestern Chihuahua. The 3 most isolated colonies are not shown on the map.

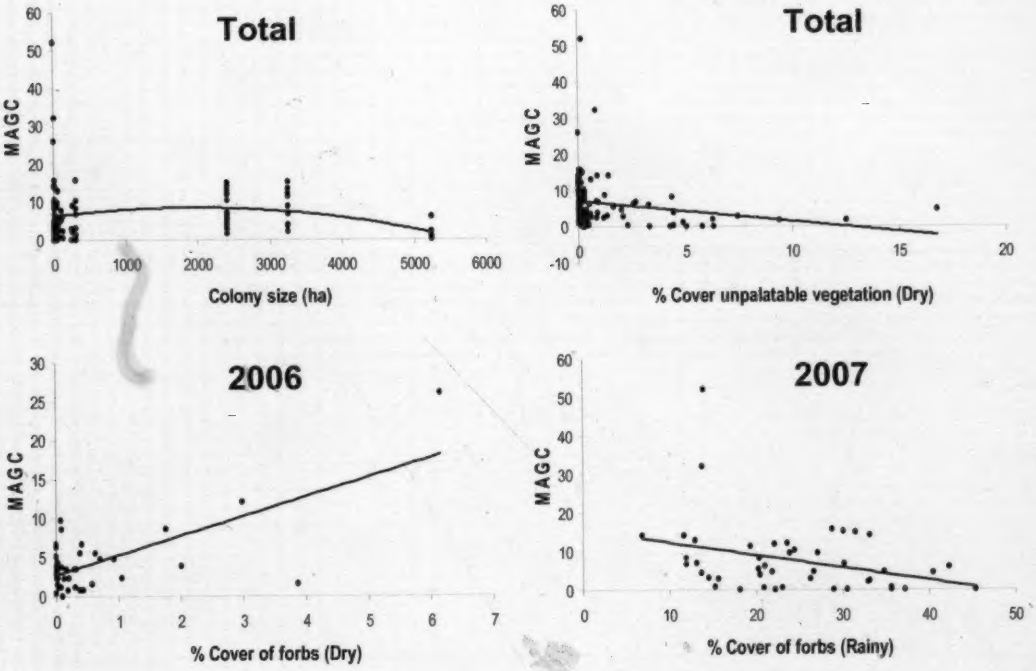


Fig. 4-2. Relationships of maximum aboveground density (MAGD) of black-tailed dogs with some of the most significant variables in best multivariable models (see Table 4). The upper graphs include pooled data from 3 years. The lower graphs include year-specific data.

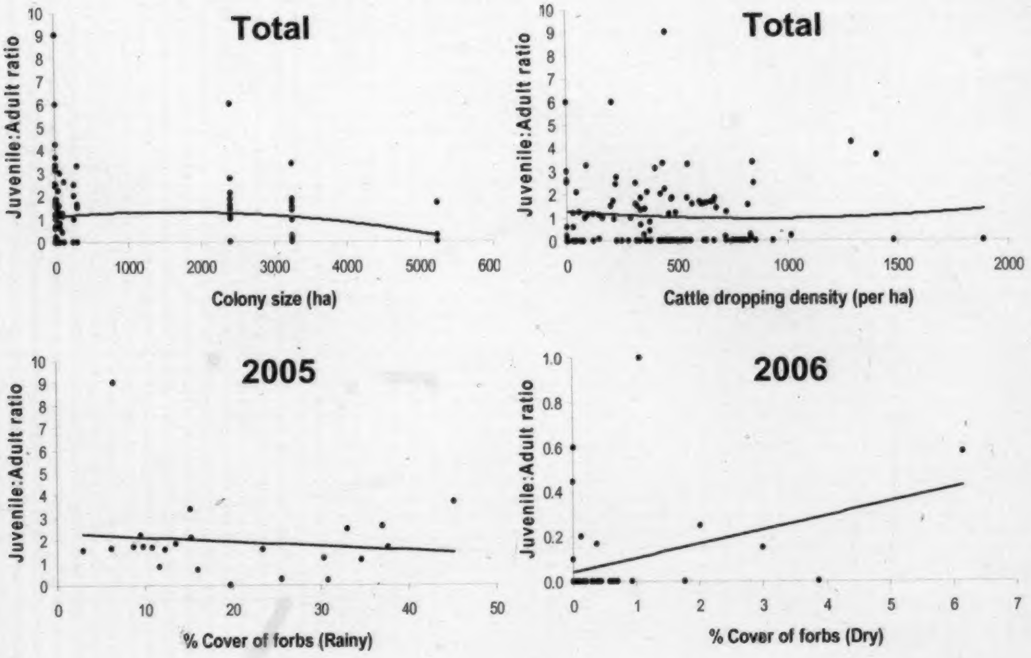


Fig. 4-3. Relationships of juvenile production of black-tailed dogs with some of the most significant variables in best multivariable models (see Table 5). The upper graphs include pooled data from 3 years. The lower graphs include year-specific data.

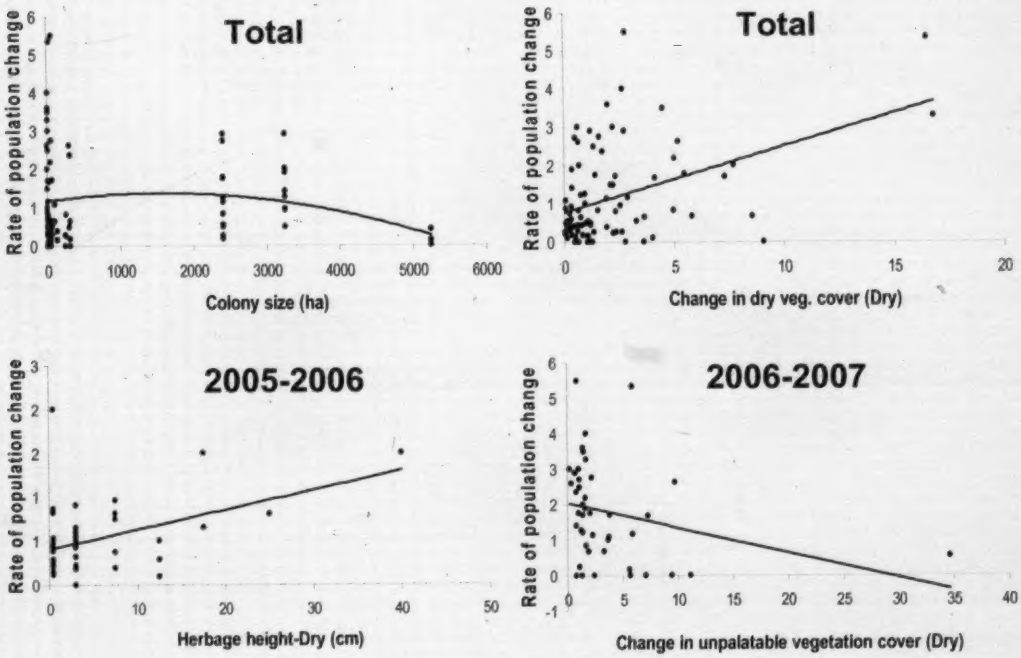


Fig. 4-4. Relationship between the rate of black-tailed prairie dog population change and some of the most significant variables in best multivariable models (see Table 6). The upper graphs include pooled data from 2 periods (2005-2006 and 2006-2007). The lower graphs include period-specific data.

Fig. 4-5

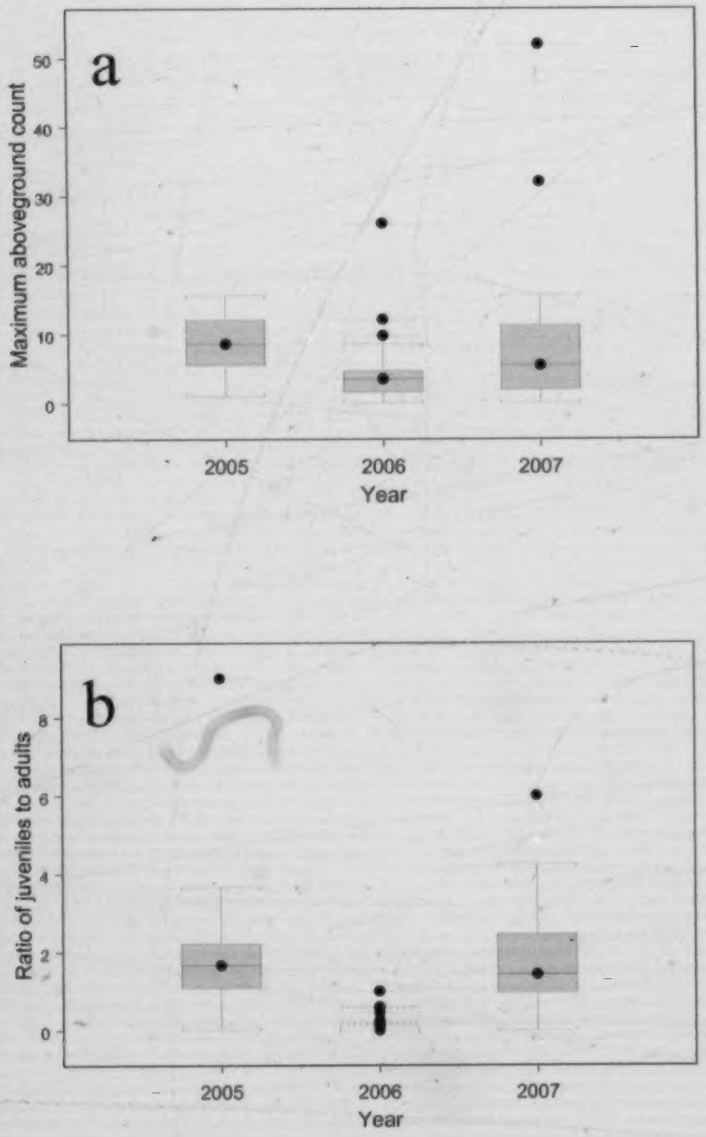
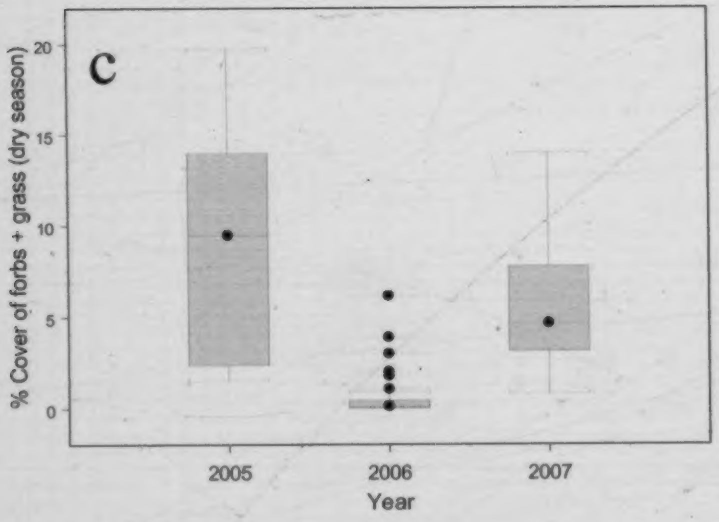

a
Maximum aboveground count
0
10
20
30
40
50
2005
2006
2007
Year
b
Ratio of juveniles to adults
0
2
4
6
8
2005
2006
2007
Year

Fig. 4-2 (continued)



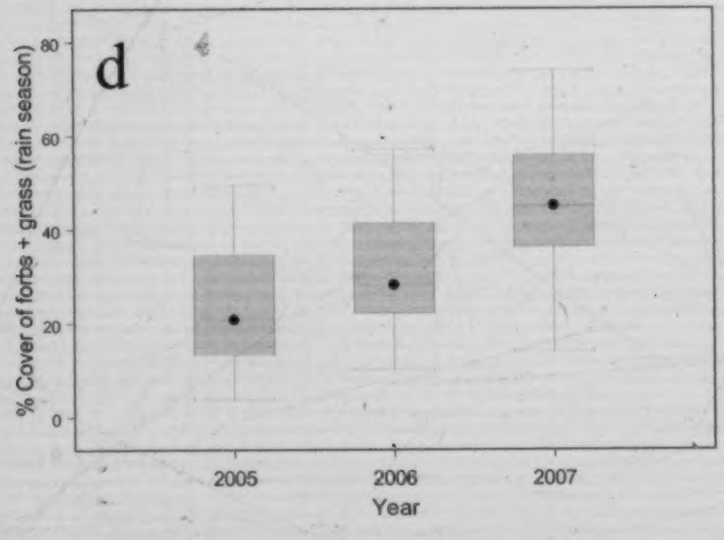


Fig. 4-5. Variation in relative density (a) and juvenile production (b) of BTPDs in northwestern Chihuahua between 2005 and 2007. Note that herbage cover during the dry season (c) but not during the rain season (d) exhibit a similar pattern of change. Boxes group data in quartiles and dots with dashed lines represent outliers.

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CHAPTER 5

GENERAL DISCUSSION

Ecological theory predicts that populations living at the edge of the species' geographic range should encounter the most challenging environmental conditions (Brown 1984, Lawton 1993). If black-tailed prairie dogs (BTPDs) fit this pattern, those populations living at the northern and southern edges of geographic distribution should face the most challenging physical environments. Because water is the most limiting resource in arid ecosystems (Brown et al. 1997), BTPD populations in southern desert grasslands may be limited by primary productivity. Overall, results of this study support the latter prediction, as patterns of occurrence and abundance of BTPDs in northwestern Chihuahua are strongly influenced by spatial and temporal variations in forage cover.

The effects of plant abundance on BTPD populations may operate in opposite directions depending on the dominant climatic context. When dryness is prevalent (either within or between years) BTPDs seem to benefit from increased plant abundance, but under more humid conditions they benefit from reduced levels of plant production. For example, during an intense period of drought, the extinction probability of BTPD colonies in Chihuahua was lower on sites with higher levels of plant abundance, but the relationship was reversed once precipitation approached average levels (Chapter 2). In a shorter temporal scale, forage cover during the dry season (late spring) was positively related with BTPD population density, juvenile production and rate of population change, but these relationships were predominantly negative during the peak of the rainy season

(Chapter 4). In reality, such contradictory results are not surprising given the opposite effects that forage has on BTPDs; whereas grasses and forbs constitute their fundamental sources of food, excessive plant growth reduces their visibility for predator detection (Hoogland 1995).

The results previously described suggest that optimal habitat for BTPDs should be one that maximizes forage cover for sustained food production while minimizing forage height for optimal visibility. Indeed, several lines of evidence suggest that this dual nature of vegetation could be the most prominent feature of the BTPD habitat. Scattered information on BTPD-habitat associations indicates that typical BTPD habitat (at least in northern locations) is characterized by short vegetation (mostly grasses) with moderate-to-high levels of cover (Clippinger 1989, Hoogland 1995, Roe and Roe 2003). Although BTPD populations in northwestern Mexico might occur at sites with much lower levels of forage cover than those previously reported (Chapter 3), my results still indicate a high dependence of BTPDs on increased levels of forage cover and low plant heights. Habitat selection models produced in this study indicate that, on a regional scale, southern BTPDs are more likely to occur on sites with sparser and shorter vegetation. This pattern suggests high habitat selectivity by BTPDs in a landscape that is dominated by dense or relatively dense shrubland communities. However, forage cover emerges as a positive predictor of occurrence once other significant environmental factors are held constant in models (Chapter 3).

Extreme climatic conditions in the Chihuahuan Desert could make numbers of BTPD populations more unstable over time. Because aridity is the prevailing condition during most of the year, desert grasslands exhibit the lowest levels of plant production among all North American grasslands (Sims et al. 1978). As a consequence of reduced primary production, desert grasslands sustain the lowest densities of BTPDs over the entire species' range (Facka et al. 2008, Truett et al. in press, this study). Such low population numbers, however, may be insufficient to control the rapid growth of forage that occurs in response to the short and intense rain events that are prevalent in the region. Under these conditions, BTPDs either move to areas with higher BTPD density or die as a consequence of increased predation. Inter-annual variation in precipitation regimes, particularly when severe periods of drought intervene, may further contribute to define numerical fluctuations in southern BTPD populations. Such climatic factors could explain why BTPDs in South Dakota (King 1955, Garrett et al. 1982, Hoogland 2006) did not exhibit sharp declines in density and juvenile production as observed in BTPD populations in New Mexico (Facka et al. 2008) and Chihuahua (Chapter 4).

The strong association of BTPDs with open areas with little cover of shrubs seems to result from their need of a high visibility to detect predators (Hoogland 1995). Therefore, it is often assumed that habitat quality is reduced with increasing abundance of shrubs within BTPD colonies (i.e. Ceballos et al. 2005). In agreement with that interpretation, my habitat selection models clearly showed that BTPDs in northwestern Chihuahua used open areas in a much higher frequency than areas with shrubs (Chapter 3). Considering that this pattern emerged in a landscape dominated by shrubland communities, modeling results could indicate real habitat selection by southern BTPD populations. In fact, it has been experimentally demonstrated that reduced cover of shrubs may be used by BTPDs as a clue to select areas of colonization (Milne-Laux and Sweitzer 2006). Surprisingly, results of this study suggest that BTPD populations in open areas do not necessarily perform better than populations in savannah areas: shrub cover was absent from best demographic models, and when it was present the relationship with demographic indices (density and juvenile production) was slightly positive (Chapter 4). It is likely that some BTPD populations shift their behavioral patterns to take advantage of the protective nature of shrubs, a phenomenon that has been observed in Uinta ground squirrels which may opportunistically use shrubs to hide from predators (Hannon et al. 2006). Alternatively, tall shrubs with large basal stems may not restrict visibility for BTPD at ground level. Some behavioral data collected in the study area seems to support the latter hypothesis: time spent in vigilance by individuals was positively related with forage height, but no relationship was observed between vigilance and shrub cover (Avila-Flores and De Villa-Meza 2006). In addition, high forage cover on sites with high cover of shrubs could help to explain the high performance of these populations.

The need of sufficient food and clear views seems to define much of the BTPD-habitat associations. Because diets of BTPDs and cattle greatly overlap (Detling 2006), overgrazing by cattle has been considered a factor that reduces habitat quality for BTPDs, particularly in low-productive regions (Ceballos et al. 2005). However, cattle grazing may indeed increase habitat quality for BTPDs by reducing the height of the herbaceous layer and increasing the nutritious value of food (Detling 2006). Based on these arguments, it has been hypothesized that livestock grazing may have promoted the historical expansions of BTPDs both in the U. S. Great Plains and the Chihuahuan Desert in northern Mexico (Vermeire et al. 2004, Forrest 2005, Truett et al. in press). However, I did not find evidence of important negative or positive impacts of cattle grazing on BTPD populations, as no patterns of habitat selection or demography were clearly explained by local differences in cattle activity (Chapters 3 and 4). Because livestock are free to move over vast territories, they can easily abandon foraging areas which have insufficient food levels for them but sufficient to support some BTPD individuals. Therefore, movement patterns of cattle may buffer the negative impacts of overgrazing in these areas of low productivity.

Landscape structure seems to play a secondary role in defining patterns of distribution and abundance of BTPDs in northwestern Chihuahua. In general, results of this study coincide with findings of previous investigations, which have shown that increased isolation, either by distance or by spatial context, may influence population performance in two opposite directions. In the long term, increased isolation may drive local BTPD populations to extinction, although it may also reduce the extinction probability of populations when sylvatic plague is present in the region (Lomolino and Smith 2001, Lomolino et al. 2003). In a shorter term, small colonies isolated by hostile habitat in the surroundings tend to support high population densities, a pattern that may result from reduced predation rates, increased isolation from plague, or reduced dispersal rates

(Johnson and Collinge 2004, Magle et al. 2007). I hypothesized that high densities in small and isolated BTPD populations in Chihuahua resulted from reduced dispersal rates caused by physical barriers in the surroundings (Chapter 4). The high probability of use by BTPDs of sites well connected to other colony areas suggests that reduced isolation may facilitate BTPD movements (Chapter 3). Whatever the cause of this pattern, it is unknown how population vital rates and persistence probability are affected by such high densities. Taken together, results of this and other studies suggest that the long-term effects of size and isolation may be context-dependent. In the case of BTPD populations in Mexico, the extinction probability of small and isolated populations may be very high during periods of severe drought (likely associated with intense food shortages), but it can be greatly reduced during milder climatic conditions (Chapter 2).

Previous studies concluded that human activities played a primary role on the collapse of BTPD populations in northwestern Chihuahua (List 1997, Marcé 2001, Ceballos et al. 2005). Based on information collected at some colonies from the center of the complex, it was suggested that habitat loss caused by agricultural activities, poisoning, and shrub encroachment associated with desertification processes were the main causes of colony losses (List 1997, Marcé 2001). However, data collected in this study failed to support the hypothesis of a human-driven population collapse. The colony area lost to agriculture and urbanization between 1988 and 2005 was close to 6%, which is sizeable area but still does not explain the large population collapse. Poisoning was a common method to control BTPD populations in the region before 2000 (R. List pers.

comm.); however, it is unlikely that 20,000-30,000 hectares of BTPD colonies were poisoned between 1988 and 2000 considering the high costs associated with poisoning and the lack of evidence (empty poison tubes) in most colonies. Active agricultural lands and other human features, however, may contribute to increase the area of hostile habitats in the surroundings and thus indirectly affect successful dispersal (Chapter 3).

Taken together, results of this study suggest that temporal changes in distribution, patterns of habitat selection, and spatial differences in demography of BTPD populations in northwestern Chihuahua are strongly associated with spatial and temporal differences in plant abundance. Because these BTPD populations seem to be highly sensitive to reductions in forage production (Chapter 4), I believe that the dramatic population decline observed in Chihuahua between 1988 and 2000 was mostly driven by the severe drought affecting the region between 1994 and 2004. Although size and isolation effects may have played a secondary role on extinction of colonies, their influence seemed to be dependent on the occurrence of drought. These results, however, alert for potential negative impacts of global warming on southern BTPD populations.

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APPENDIX I

Pairwise correlation matrices for variables describing environmental and landscape attributes of 25-ha cells at the beginning of each period of analyses. Bold numbers indicate correlations higher than 0.7. NDVI = normalized difference vegetation index, %Gr = percent area covered by grasslands, %Sh = percent area covered by shrublands, %BL = percent area covered by barren lands, CS = colony size, AH3 = area covered by hostile habitat within 3 km, and AC3 = area covered by prairie dog colonies within 3 km. The following attributes represent rates of change by the end of each period: AA-Ch = proportion of cell area that changed to active agriculture, IA-Ch = proportion of cell area that changed to inactive agriculture, UL-Ch = proportion of cell area that changed to urban use.

1988-2000

	NDVI	%Gr	%Sh	%BL	AA-Ch	IA-Ch	UL-Ch	CS	AH3	AC3
NDVI	1.00	-0.25	0.20	-0.13	-0.12	0.00	0.03	0.13	0.05	0.08
%Gr	-0.25	1.00	**-0.80**	-0.39	0.08	0.05	-0.02	0.30	-0.38	0.25
%Sh	0.20	**-0.80**	1.00	-0.06	-0.03	0.02	0.03	-0.30	0.38	-0.22
%BL	-0.13	-0.39	-0.06	1.00	-0.01	-0.02	0.01	-0.13	-0.04	-0.09
AA-Ch	-0.12	0.08	-0.03	-0.01	1.00	0.02	0.00	-0.08	0.00	-0.03
IA-Ch	0.00	0.05	0.02	-0.02	0.02	1.00	0.00	-0.22	0.27	-0.07
UL-Ch	0.03	-0.02	0.03	0.01	0.00	0.00	1.00	-0.01	-0.05	0.01
CS	0.13	0.30	-0.30	-0.13	-0.08	-0.22	-0.01	1.00	-0.35	0.61
AH3	0.05	-0.38	0.38	-0.04	0.00	0.27	-0.05	-0.35	1.00	-0.50
AC3	0.08	0.25	-0.22	-0.09	-0.03	-0.07	0.01	0.61	-0.50	1.00

2000-2005

	NDVI	%Gr	%Sh	%BL	AA-Ch	IA-Ch	UL-Ch	CS	AH3	AC3
NDVI	1.00	-0.41	0.15	-0.07	-0.20	0.11	-0.02	0.03	0.28	-0.19
%Gr	-0.41	1.00	-0.52	-0.06	-0.08	0.22	-0.02	0.18	-0.67	0.21
%Sh	0.15	-0.52	1.00	-0.02	-0.02	0.01	0.05	-0.31	0.42	-0.25
%BL	-0.07	-0.06	-0.02	1.00	-0.01	-0.01	-0.01	-0.10	-0.04	-0.09
AA-Ch	-0.20	-0.08	-0.02	-0.01	1.00	-0.04	0.00	0.09	0.10	0.01
IA-Ch	0.11	0.22	0.01	-0.01	-0.04	1.00	-0.01	-0.03	0.10	-0.20
UL-Ch	-0.02	-0.02	0.05	-0.01	0.00	-0.01	1.00	-0.08	0.07	-0.07

CS	0.03	0.18	-0.31	-0.10	0.09	-0.03	-0.08	1.00	-0.40	0.78
AH3	0.28	-0.67	0.42	-0.04	0.10	0.10	0.07	-0.40	1.00	-0.49
AC3	-0.19	0.21	-0.25	-0.09	0.01	-0.20	-0.07	0.78	-0.49	1.00

APPENDIX II

Pairwise correlation matrices for variables describing environmental and landscape attributes of focal colonies at the beginning of each period of analyses. Bold numbers indicate correlations higher than 0.7. CS = colony size, NC3 = number of colonies within 3 km, NDVI = normalized difference vegetation index, %Gr = percent area covered by grasslands, %Sh = percent area covered by shrublands, %BL = percent area covered by barren lands. The following attributes represent rates of change by the end of each period: AA-Ch = proportion of cell area that changed to active agriculture, IA-Ch = proportion of cell area that changed to inactive agriculture, UL-Ch = proportion of cell area that changed to urban use.

1988-2000

	CS	NC3	NDVI	%Gr	%Sh	AA-Ch	IA-Ch	UL-Ch	%BL
CS	1.00	0.23	0.24	0.23	-0.21	0.01	0.09	**-0.98**	-0.05
NC3	0.23	1.00	0.10	-0.03	-0.04	0.15	-0.12	-0.14	0.17
NDVI	0.24	0.10	1.00	0.35	-0.21	-0.05	0.30	-0.19	-0.35
%Gr	0.23	-0.03	0.35	1.00	**-0.92**	0.11	0.15	-0.19	-0.11
%Sh	-0.21	-0.04	-0.21	**-0.92**	1.00	-0.09	-0.15	0.17	-0.28
AA-Ch	0.01	0.15	-0.05	0.11	-0.09	1.00	0.15	0.04	-0.08
IA-Ch	0.09	-0.12	0.30	0.15	-0.15	0.15	1.00	0.02	-0.04
UL-Ch	**-0.98**	-0.14	-0.19	-0.19	0.17	0.04	0.02	1.00	0.05
%BL	-0.05	0.17	-0.35	-0.11	-0.28	-0.08	-0.04	0.05	1.00

2000-2005

	CS	NC3	NDVI	%Gr	%Sh	AA-Ch	IA-Ch	UL-Ch	%BL
CS	1.00	-0.16	-0.04	0.06	-0.07	0.06	-0.04	-0.04	0.01
NC3	-0.16	1.00	0.03	0.37	-0.30	0.04	0.24	0.08	-0.05
NDVI	-0.04	0.03	1.00	-0.23	0.37	-0.24	-0.10	-0.10	-0.20
%Gr	0.06	0.37	-0.23	1.00	**-0.74**	-0.17	0.24	0.08	0.03
%Sh	-0.07	-0.30	0.37	**-0.74**	1.00	0.32	-0.21	-0.06	-0.04
AA-Ch	0.06	0.04	-0.24	-0.17	0.32	1.00	-0.17	0.06	0.02
IA-Ch	-0.04	0.24	-0.10	0.24	-0.21	-0.17	1.00	-0.08	-0.07
UL-Ch	-0.04	0.08	-0.10	0.08	-0.06	0.06	-0.08	1.00	-0.03
%BL	0.01	-0.05	-0.20	0.03	-0.04	0.02	-0.07	-0.03	1.00

APPENDIX III

Attributes of focal colonies for the period 1988-2000.

Name in 1988	Status by 2000	Area 1988	Area 2000	# Fragments by 2000	% Change by 2000	# Colonies within 3 km	NDVI
Buenos Aires	Reduced	2306.0	1017.9	3	-55.9	2	0.092
El Cuervo	Reduced	31497.1	15520.7	1	-50.7	2	0.096
Loma Los Ratones	Reduced	4650.2	1220.3	8	-73.8	5	0.074
Nifay SW	Reduced	119.8	56.7	1	-52.7	2	0.053
Ojitos	Reduced	444.4	210.6	1	-52.6	1	0.142
Pancho Villa	Reduced	3021.6	539.3	5	-82.2	0	0.110
Salto de Ojo	Reduced	1969.2	1249.1	2	-36.6	2	0.053
San Blas	Reduced	37.2	17.7	1	-52.6	1	0.146
El Berrendo	Extinct	10.2	0.0	0	-100.0	0	0.022
La Cal	Extinct	6.1	0.0	0	-100.0	0	0.025
El Moris	Extinct	8.1	0.0	0	-100.0	0	0.013
San Francisco	Extinct	138.3	0.0	0	-100.0	0	0.075
Los Mimbres	Extinct	71.6	0.0	0	-100.0	1	0.031
Madera	Extinct	13.8	0.0	0	-100.0	2	0.061
Buenavista	Extinct	9.0	0.0	0	-100.0	2	0.053
Los Tecolotes	Extinct	6.4	0.0	0	-100.0	1	0.088
El Carrizo	Extinct	9.5	0.0	0	-100.0	0	0.079
San Rafael	Extinct	69.4	0.0	0	-100.0	2	-0.021
Sierra de Enmedio	Extinct	33.2	0.0	0	-100.0	1	0.061
San Rafael E	Extinct	15.9	0.0	0	-100.0	1	0.018
El Peñasco	Extinct	114.7	0.0	0	-100.0	0	0.026
San Basilio	Extinct	5.9	0.0	0	-100.0	0	0.039
San Pedro S	Extinct	46.6	0.0	0	-100.0	3	0.062

APPENDIX III (continued)

Name in 1988	% Grassland	% Shrubland	% Barren land	% Change (by 2000) in: Active agriculture	Inactive agriculture	Urban area
Buenos Aires	79.4	1.7	17.1	-0.1	9.6	0.0
El Cuervo	92.6	3.9	2.0	0.1	1.7	0.0
Loma Los Ratones	79.8	16.7	3.6	0.0	0.0	0.0
Niñay SW	99.8	0.0	0.2	0.0	0.0	0.0
Ojitos	92.1	5.1	2.8	0.0	0.0	0.0
Pancho Villa	75.3	21.9	0.0	-0.4	31.0	0.0
Salto de Ojo	80.2	16.1	0.0	8.3	8.5	0.0
San Blas	100.0	0.0	0.0	0.0	0.0	0.0
El Berrendo	75.6	24.4	0.0	0.0	0.0	0.0
La Cal	100.0	0.0	0.0	0.0	0.0	0.0
El Moris	46.8	53.2	0.0	0.0	0.0	0.0
San Francisco	94.7	4.1	1.2	0.0	0.0	0.0
Los Mimbres	0.0	100.0	0.0	0.0	0.0	0.0
Madera	45.6	54.4	0.0	0.0	0.0	0.0
Buenavista	2.7	97.3	0.0	0.0	0.0	0.0
Los Tecolotes	84.1	0.0	15.9	0.0	0.0	0.0
El Carrizo	8.0	92.0	0.0	0.0	0.0	0.0
San Rafael	28.5	4.2	67.3	0.0	0.0	0.0
Sierra de Enmedio	54.9	45.1	0.0	0.0	0.0	0.0
San Rafael E	97.1	2.9	0.0	0.0	0.0	0.0
El Peñasco	66.3	25.1	8.6	0.0	0.0	0.0
San Basilio	8.3	91.7	0.0	0.0	0.0	0.0
San Pedro S	4.5	95.5	0.0	0.0	0.0	0.0

[1] Percent change reported in relation to initial area of colony. Negative numbers indicate an area reduction in land use cover types within colonies

APPENDIX IV

Attributes of focal colonies for the period 2000-2005.

Name in 2000	Status by 2005	Area 2000	Area 2005	# Fragments by 2005	% Change by 2005	# Colonies within 3 km	NDVI
Ampliación Pancho Villa	Expanded	938.2	1404.8	1	49.7	1	-0.035
Buenos Aires	Reduced	580.4	395.8	4	-31.8	2	-0.040
El Aguila	Expanded	183.3	303.4	1	65.5	6	-0.037
El Apache	Stable	20.1	15.6	1	-22.4	2	-0.021
El Cuervo	Reduced	15520.7	6254.6	10	-59.7	1	-0.025
El Gavilán N1	Expanded	7.2	56.6	1	683.8	9	-0.011
El Gavilán N2	Reduced	8.8	0.9	1	-89.6	6	-0.014
El Gavilán NE	Reduced	42.7	11.8	2	-72.4	8	-0.029
El Gavilán S	Stable	38.6	39.3	2	1.8	9	-0.020
El Monte	Expanded	3.8	9.8	1	155.7	1	-0.018
El Uno N	Stable	33.4	36.1	1	8.1	9	-0.009
El Uno S1	Expanded	6.7	19.0	1	184.7	4	-0.021
El Uno SSE	Reduced	40.9	16.8	1	-59.0	4	-0.051
El Uno-La Báscula S	Stable	1.2	1.0	1	-16.2	3	-0.040
La Cal E	Expanded	2.0	29.7	1	1365.7	4	0.033
La Cal W	Stable	13.2	15.2	1	15.1	1	0.006
La Ciénega W	Expanded	1.4	15.9	1	1042.2	3	0.011
Los Alisios	Expanded	0.3	0.9	1	261.9	1	-0.038
Los Bejucos	Stable	228.7	208.5	2	-8.8	2	-0.033
Los Bejucos S	Reduced	21.2	1.7	1	-91.8	4	-0.016
Los Bejucos SW	Expanded	2.0	43.2	1	2041.1	6	-0.042
Los Nogales	Reduced	10.2	2.1	1	-79.6	1	-0.034
Los Ratones S	Stable	13.0	10.4	1	-20.4	2	-0.057
Los Ratones SW	Expanded	34.5	63.2	1	83.2	2	-0.033
Monte Verde	Reduced	94.2	59.0	2	-37.3	2	-0.021
Nevarez	Reduced	101.9	57.7	1	-43.4	2	-0.044
Nifay SW	Stable	56.7	43.2	1	-23.8	1	-0.032
Ojitos S	Stable	228.3	246.7	1	8.1	0	-0.033
Pancho Villa E1	Reduced	75.8	2.5	1	-96.6	5	-0.022
Pancho Villa E2	Reduced	0.5	0.3	1	-32.4	6	-0.027
Pancho Villa N	Stable	291.4	309.9	1	6.3	6	-0.034
Pancho Villa NE1	Reduced	14.2	1.7	1	-87.8	5	-0.038
Pancho Villa NE2	Expanded	6.9	11.1	2	60.5	6	-0.040
Papalote de San Pedro	Expanded	3.0	8.0	1	171.0	7	0.002
Rogelio	Stable	10.1	9.9	1	-2.5	2	-0.040
Salto de Ojo-La Báscula	Stable	1271.6	999.9	1	-21.4	10	-0.036
San Pedro N	Reduced	9.6	3.1	1	-67.9	7	-0.011
Santa Anita NE	Expanded	1.5	89.8	1	5732.7	3	0.021
Tierras Prietas	Reduced	396.6	255.0	1	-35.7	3	-0.049
El Gavilán E	Extinct	7.9	0.0	0	-100.0	6	-0.024

La Ciénega NW	Extinct	37.4	0.0	0	-100.0	4	-0.008
Monteverde S	Extinct	17.0	0.0	0	-100.0	4	-0.018
Pancho Villa W	Extinct	56.1	0.0	0	-100.0	0	0.030

APPENDIX IV (continued)

Name in 2000	% Grassland	% Shrubland	% Barren land	% Change (by 2005) in[1]: Active agriculture	Inactive agriculture	Urban area
Ampliación Pancho Villa	73.4	26.6	0.0	0.0	0.0	0.0
Buenos Aires	99.6	0.4	0.0	0.0	28.8	0.0
El Aguila	100.0	0.0	0.0	0.0	0.0	0.0
El Apache	89.8	10.2	0.0	0.0	0.0	0.0
El Cuervo	90.7	2.7	0.1	0.9	3.0	0.0
El Gavilán N1	100.0	0.0	0.0	0.0	0.0	0.0
El Gavilán N2	99.9	0.2	0.0	0.0	15.7	0.0
El Gavilán NE	99.4	0.6	0.0	0.0	63.0	0.0
El Gavilán S	82.9	10.4	0.0	0.0	31.9	0.0
El Monte	40.7	59.3	0.0	0.0	0.0	0.0
El Uno N	100.0	0.0	0.0	0.0	0.0	0.0
El Uno S1	100.0	0.0	0.0	0.0	8.2	0.0
El Uno SSE	100.0	0.0	0.0	0.0	66.6	0.0
El Uno-La Báscula S	100.0	0.0	0.0	0.0	0.0	0.0
La Cal E	13.7	86.4	0.0	0.0	0.0	0.0
La Cal W	15.6	84.4	0.0	0.0	0.0	0.0
La Ciénega W	64.7	35.3	0.0	0.0	0.0	0.0
Los Alisios	100.0	0.0	0.0	0.0	0.0	0.0
Los Bejucos	61.0	39.1	0.0	0.0	0.0	0.0
Los Bejucos S	99.8	0.3	0.0	0.0	0.0	0.0
Los Bejucos SW	100.0	0.0	0.0	0.0	0.0	0.0
Los Nogales	41.1	58.9	0.0	0.0	0.0	0.0
Los Ratones S	100.0	0.0	0.0	0.0	0.0	0.0
Los Ratones SW	96.9	3.1	0.0	0.0	0.0	0.0
Monte Verde	0.9	95.5	0.0	11.3	-0.1	4.6
Nevarez	0.0	0.0	0.0	0.0	-11.3	0.0
Nifay SW	99.9	0.1	0.0	0.0	0.0	0.0
Ojitos S	99.4	0.6	0.0	0.0	0.0	0.0
Pancho Villa E1	100.0	0.0	0.0	0.0	0.0	0.0
Pancho Villa E2	100.0	0.0	0.0	-14.5	0.0	0.0
Pancho Villa N	88.1	5.9	0.0	0.0	43.4	0.6
Pancho Villa NE1	100.0	0.0	0.0	0.0	0.0	57.0
Pancho Villa NE2	100.0	0.0	0.0	0.0	77.8	0.0
Papalote de San Pedro	100.0	0.0	0.0	0.0	0.0	0.0
Rogelio	0.0	0.0	0.0	-1.4	0.0	0.0
Salto de Ojo-La Báscula	90.9	7.6	0.2	0.0	14.8	0.0
San Pedro N	85.8	0.0	0.0	0.0	0.0	7.5
Santa Anita NE	82.5	17.5	0.0	0.0	0.0	0.0
Tierras Prietas	84.9	8.7	6.4	0.0	0.0	0.0

El Gavilán E	93.9	0.0	0.0	0.0	-3.7	0.0
La Ciénega NW	100.0	0.0	0.0	0.0	0.0	0.0
Monteverde S	32.7	67.3	0.0	0.0	0.0	0.0
Pancho Villa W	68.8	0.7	0.0	-17.0	44.3	0.0

[1] Percent change reported in relation to initial area of colony. Negative numbers indicate an area reduction in land use cover types within colonies

APPENDIX V

Pairwise correlation matrix for variables describing local and landscape attributes of 151 used and 133 unsed sites. Bold numbers indicate correlations higher than 0.7. H = herbage height, S = slope, A = altitude, SC = percent cover of shrubs, SD = shrub density, C = cattle dropping density, D = dry vegetation cover, U = unpalatable vegetation cover, F = forb cover, G = grass cover, B = bare ground cover, C1 and C3 = are covered by prairie dog colonies within 1 and 3 km, H1 and H3 = area covered by hostile habitat within 1 and 3 km, R1 and R3 = road density within 1 and 3 km, M = soil moisture regime, DT = distance to nearest town, DR = distance to nearest main road.

	H	S	A	SC	SD	C	D	U	F	G
H	1.00	0.04	-0.07	0.14	0.10	-0.17	0.04	0.19	0.11	0.60
S	0.04	1.00	0.43	0.19	0.31	-0.04	-0.03	-0.03	0.06	0.10
A	-0.07	0.43	1.00	-0.15	-0.02	-0.04	-0.10	0.00	0.07	0.00
SC	0.14	0.19	-0.15	1.00	0.65	-0.02	0.09	0.11	-0.08	0.09
SD	0.10	0.31	-0.02	0.65	1.00	-0.01	0.05	0.03	-0.03	0.03
C	-0.17	-0.04	-0.04	-0.02	-0.01	1.00	-0.18	-0.15	-0.02	0.08
D	0.04	-0.03	-0.10	0.09	0.05	-0.18	1.00	-0.01	-0.22	-0.01
U	0.19	-0.03	0.00	0.11	0.03	-0.15	-0.01	1.00	-0.14	-0.13
F	0.11	0.06	0.07	-0.08	-0.03	-0.02	-0.22	-0.14	1.00	-0.13
G	0.60	0.10	0.00	0.09	0.03	0.08	-0.01	-0.13	-0.13	1.00
B	-0.65	-0.11	-0.03	-0.08	-0.02	0.07	-0.11	-0.20	-0.53	-0.62
C1	-0.29	-0.22	-0.10	-0.24	-0.19	0.11	-0.09	-0.19	-0.04	-0.14
C3	-0.24	-0.21	-0.07	-0.20	-0.17	0.14	-0.09	-0.17	0.02	-0.13
H1	0.26	-0.06	-0.30	0.21	0.11	-0.09	0.01	0.12	0.18	0.02
H3	0.21	-0.09	-0.39	0.26	0.18	0.05	-0.03	0.10	0.04	0.07
R1	0.06	-0.03	-0.12	0.09	0.13	-0.03	-0.03	0.05	-0.06	-0.10
R3	0.01	-0.10	-0.20	-0.03	0.04	0.00	-0.06	0.00	-0.10	-0.08
M	0.01	0.17	0.60	-0.04	-0.07	-0.02	0.01	0.06	0.17	-0.01
DT	0.05	0.11	-0.04	0.02	0.01	-0.08	0.00	0.09	-0.04	0.05

DR	0.07	0.17	0.18	0.11	0.01	0.12	0.00	0.06	0.10	0.10

APPENDIX V (continued)

	B	C1	C3	H1	H3	R1	R3	M	DT	DR
H	-0.65	-0.29	-0.24	0.26	0.21	0.06	0.01	0.01	0.05	0.07
S	-0.11	-0.22	-0.21	-0.06	-0.09	-0.03	-0.10	0.17	0.11	0.17
A	-0.03	-0.10	-0.07	-0.30	-0.39	-0.12	-0.20	0.60	-0.04	0.18
SC	-0.08	-0.24	-0.20	0.21	0.26	0.09	-0.03	-0.04	0.02	0.11
SD	-0.02	-0.19	-0.17	0.11	0.18	0.13	0.04	-0.07	0.01	0.01
C	0.07	0.11	0.14	-0.09	0.05	-0.03	0.00	-0.02	-0.08	0.12
D	-0.11	-0.09	-0.09	0.01	-0.03	-0.03	-0.06	0.01	0.00	0.00
U	-0.20	-0.19	-0.17	0.12	0.10	0.05	0.00	0.06	0.09	0.06
F	-0.53	-0.04	0.02	0.18	0.04	-0.06	-0.10	0.17	-0.04	0.10
G	-0.62	-0.14	-0.13	0.02	0.07	-0.10	-0.08	-0.01	0.05	0.10
B	1.00	0.25	0.19	-0.22	-0.13	0.10	0.15	-0.15	-0.04	-0.18
C1	0.25	1.00	**0.81**	-0.27	-0.27	-0.12	0.03	-0.13	0.01	-0.10
C3	0.19	**0.81**	1.00	-0.25	-0.30	-0.09	0.03	-0.14	0.01	-0.08
H1	-0.22	-0.27	-0.25	1.00	**0.78**	0.10	0.00	0.07	-0.20	-0.06
H3	-0.13	-0.27	-0.30	**0.78**	1.00	0.13	0.12	0.02	-0.25	-0.16
R1	0.10	-0.12	-0.09	0.10	0.13	1.00	0.66	-0.10	-0.04	-0.40
R3	0.15	0.03	0.03	0.00	0.12	0.66	1.00	-0.25	-0.13	-0.58
M	-0.15	-0.13	-0.14	0.07	0.02	-0.10	-0.25	1.00	-0.15	0.20
DT	-0.04	0.01	0.01	-0.20	-0.25	-0.04	-0.13	-0.15	1.00	0.24
DR	-0.18	-0.10	-0.08	-0.06	-0.16	-0.40	-0.58	0.20	0.24	1.00

APPENDIX VI

Biological attributes measured over time at 45 sampling plots. TD = total relative density of prairie dogs, AD = adult relative density of prairie dogs, J/A = juvenile to adult ratio, Ct = cattle activity, Pr = incidence of predators, Sh = shrub obstruction index, HHD and HHR = herbage height in dry and rain seasons, DVD and DVR = dry vegetation cover in dry and rain seasons, UVD and UVR = unpalatable vegetation cover in dry and rain seasons, FbD and FbR = forbs cover in dry and rain seasons, GsD and GsR = grass cover in dry and rain seasons.

Plot name	Year	TD	AD	J/A	Ct	Pr	Sh	HHR	DVR	UVR	FbR	GsR	HHD	DVD	UVD	FbD	GsD
Agua Blanca	2006	26.0	19.0	0.6	31	0	0.0	—	0.0	0.0	23.6	0.4	0.5	0.0	0.0	6.2	0.0
	2007	52.0	17.0	2.5	0	0	0.0	2.3	0.0	0.7	13.9	3.1	1.6	3.3	0.2	5.7	0.0
Ampliación Pancho Villa E	2006	3.5	3.5	0.0	250	4	0.0	—	3.1	0.0	30.2	22.5	3.0	26.6	0.6	0.0	0.0
	2007	10.2	3.9	2.1	366	0	0.0	11.8	0.1	0.2	24.5	33.0	1.6	31.6	0.2	0.7	0.1
Ampliación Pancho Villa N	2005	12.1	4.7	1.6	609	3	0.8	—	0.0	0.0	23.4	6.2	—	1.4	0.0	13.8	0.3
	2006	6.6	6.6	0.0	559	2	0.8	—	2.3	0.0	27.4	20.5	3.0	5.7	0.0	0.4	0.0
	2007	11.7	5.5	1.4	678	3	1.5	16.9	0.0	0.0	22.1	51.4	2.1	33.2	0.0	2.4	0.1
Ampliación Pancho Villa S	2006	1.6	1.6	0.0	500	0	0.0	—	1.9	0.0	25.8	8.6	3.0	5.3	0.0	0.0	0.0
	2007	2.7	0.4	6.0	205	0	0.5	14.7	0.0	0.0	15.6	28.3	1.7	7.7	0.6	1.3	0.0
Buenos Aires	2005	6.3	2.0	2.6	0	0	0.0	—	0.0	0.0	37.0	5.8	—	6.7	0.5	8.2	9.4
	2006	2.3	2.3	0.0	472	3	0.0	—	2.4	2.7	31.7	12.1	7.5	13.4	0.0	0.0	0.0
	2007	0.4	0.4	0.0	63	0	0.2	18.7	0.0	1.8	23.0	51.3	3.5	14.4	2.3	5.7	3.3
El Aguila	2006	3.1	3.1	0.0	447	2	0.1	—	0.2	0.9	18.5	3.8	0.5	1.1	0.0	0.0	0.0
	2007	8.2	3.9	1.5	200	0	0.0	9.2	0.1	0.1	11.9	23.0	3.3	7.9	4.4	4.3	0.1
El Apache	2005	10.5	2.3	3.7	1406	1	661.0	—	0.0	0.0	45.2	10.2	—	10.5	0.0	16.4	3.6
	2006	8.6	8.6	0.0	1481	1	286.9	—	2.7	1.9	34.3	19.2	7.5	16.5	0.0	1.8	0.0
	2007	4.7	1.6	2.5	848	1	611.6	16.4	0.1	10.3	26.7	39.7	4.1	18.2	16.8	10.5	1.5
El Centro 1	2005	13.3	3.1	3.4	844	0	31.0	—	0.0	0.0	15.2	1.1	—	17.8	0.0	13.9	0.7
	2006	12.1	10.5	0.1	834	0	32.9	—	2.6	0.1	21.9	6.8	3.0	5.2	0.0	3.0	0.0
	2007	15.2	7.4	1.4	353	0	24.4	3.8	0.3	0.0	30.1	11.2	2.0	5.0	0.2	6.4	0.0
El Centro 2	2005	7.0	2.7	1.7	211	2	7.4	—	0.0	0.0	9.8	3.7	—	12.1	0.0	7.7	0.7
	2006	3.5	3.5	0.0	278	0	17.5	—	1.4	4.6	24.0	1.3	12.5	14.8	0.4	0.3	0.0
	2007	6.6	2.3	1.8	545	0	23.3	8.4	0.8	20.8	11.9	2.2	2.3	5.1	0.9	2.1	0.7
El Centro 3	2005	2.0	2.0	0.2	1016	0	0.4	—	0.0	0.0	30.8	0.9	—	4.5	0.0	15.1	0.0
	2006	3.9	3.1	0.3	831	0	0.5	—	1.5	0.0	15.3	3.5	0.5	3.0	0.3	2.0	0.0
	2007	11.3	4.7	1.5	322	0	0.6	3.2	0.2	0.1	19.3	11.5	3.8	9.1	0.0	3.1	0.0
El Centro 4	2006	8.6	8.6	0.0	825	1	309.4	—	0.8	0.3	12.5	17.5	7.5	21.1	0.3	0.1	0.0
	2007	12.1	7.4	0.9	214	0	301.6	5.8	0.3	1.6	23.6	13.8	2.8	7.2	0.1	1.0	3.0
El Cuervo E	2005	5.9	2.3	1.7	656	0	0.7	—	0.0	0.8	37.7	1.4	—	22.0	0.0	5.0	0.6

	2006	0.8	0.8	0.0	722	1	0.0	---	2.0	0.5	30.8	9.4	0.5	10.7	0.4	0.4	0.1
	2007	0.0	0.0	0.0	482	0	0.1	21.6	0.0	0.8	37.2	57.6	3.4	13.0	0.2	10.0	2.4
El Cuervo N	2005	2.0	1.6	0.3	352	2	2.0	---	0.0	0.1	25.6	11.4	---	22.7	0.0	4.9	0.7
	2006	0.0	0.0	0.0	794	0	1.8	---	1.1	0.7	35.3	6.7	3.0	10.9	0.3	0.1	0.0
	2007	0.4	0.4	0.0	76	0	4.2	25.8	0.0	0.7	35.7	52.5	11.0	32.1	4.5	8.9	5.6
El Cuervo S1	2006	2.3	2.0	0.2	0	0	0.0	---	6.2	3.1	36.1	1.1	7.5	11.4	0.9	0.1	0.0
	2007	2.7	0.4	6.0	0	0	128.3	17.0	0.0	0.2	26.3	42.5	6.7	33.7	7.5	2.9	0.2
El Cuervo S2	2006	3.5	3.5	0.0	769	2	125.4	---	2.1	0.0	31.1	8.8	3.0	8.7	0.0	0.0	0.0
	2007	5.9	2.7	1.1	464	0	122.4	14.3	0.8	6.4	42.3	12.3	2.7	37.6	3.3	2.4	0.6
El Cuervo W	2006	0.8	0.8	0.0	634	1	0.0	---	2.0	0.1	30.9	0.3	0.5	6.7	0.1	0.4	0.0
	2007	0.0	0.0	0.0	228	0	0.2	13.4	0.1	1.1	45.4	21.0	2.0	4.3	0.3	8.6	0.0
El Gavilán E	2006	3.9	3.9	0.1	147	0	23.1	---	2.3	25.9	6.7	3.3	3.0	8.1	0.9	0.0	0.0
	2007	14.1	3.5	3.3	438	0	40.5	16.3	0.3	6.2	6.8	36.9	1.7	16.9	1.4	1.8	0.1
El Gavilán N1	2006	4.7	4.7	0.0	784	0	0.0	---	1.8	2.4	17.8	30.8	0.5	13.1	0.0	0.7	0.0
	2007	12.9	5.5	1.6	567	1	0.0	20.5	0.1	0.4	12.9	56.2	4.6	21.3	0.6	6.1	1.0
El Gavilán NE	2006	2.3	2.3	0.0	459	0	48.3	---	2.3	25.9	6.7	3.3	3.0	4.7	0.2	0.2	0.0
	2007	0.0	0.0	0.0	750	0	35.7	25.8	0.0	15.5	18.2	34.9	3.7	18.3	3.3	3.1	0.3
El Gavilán S	2005	8.6	3.9	1.6	313	1	0.6	---	0.0	0.0	12.3	0.3	---	23.7	1.2	2.2	0.1
	2006	4.3	4.3	0.0	420	1	0.6	---	3.2	2.3	10.6	16.8	3.0	4.8	0.0	0.0	0.0
	2007	9.4	4.7	1.6	616	0	0.9	19.7	0.3	8.8	23.9	41.4	7.0	26.1	0.3	9.3	0.4
El Toro	2005	7.8	4.3	1.1	148	2	1.6	---	0.0	0.0	34.6	0.0	---	5.9	0.3	10.2	0.4
	2006	5.1	3.5	0.4	378	0	1.2	---	1.9	23.8	22.9	4.4	17.5	22.9	0.1	0.0	0.0
	2007	5.5	3.5	1.2	723	1	1.0	3.6	0.0	10.7	20.3	1.5	1.6	1.5	1.6	1.1	0.2
El Uno N	2006	1.2	1.2	0.0	316	0	0.0	---	0.6	0.8	20.8	1.9	0.5	1.0	0.0	0.1	0.0
	2007	6.3	3.1	1.3	58	1	0.6	14.1	0.7	1.5	21.0	30.3	5.4	23.9	2.6	6.5	0.6
El Uno S1	2005	13.7	5.5	1.7	667	0	1.4	---	0.0	0.0	8.7	1.4	---	21.5	0.0	2.3	0.0
	2006	5.5	4.7	0.2	718	0	0.7	---	0.1	0.0	20.1	16.0	0.5	2.6	0.0	0.4	0.0
	2007	0.0	4.3	1.8	478	2	0.0	14.9	0.0	2.5	29.0	38.3	2.5	27.7	4.3	4.6	0.1
La Báscula E	2005	14.1	5.1	2.1	47	2	0.0	---	0.0	0.0	15.3	1.3	---	5.5	0.0	8.4	0.4
	2006	3.5	3.5	0.0	122	2	0.4	---	1.6	0.0	24.3	19.4	0.5	13.7	0.0	0.2	0.0
	2007	4.3	2.7	1.0	85	0	0.1	19.6	0.7	0.3	13.7	41.0	5.3	10.2	0.2	6.7	1.2
La Báscula W	2005	12.9	4.7	1.8	336	0	18.9	---	0.0	0.0	13.5	0.5	---	11.8	0.1	10.8	0.9
	2006	6.3	6.3	0.0	472	0	21.6	---	0.8	0.0	19.8	33.8	0.5	11.4	0.1	0.0	0.1
	2007	7.0	3.9	1.1	94	1	4.8	23.9	0.0	0.0	13.1	58.4	7.3	22.5	0.9	10.8	4.0
La Báscula-Pipa	2006	5.5	5.5	0.0	380	1.5	0.0	---	0.2	0.0	39.5	2.0	0.5	4.4	0.1	0.6	0.0
	2007	14.8	4.3	2.7	228	0	0.2	10.7	0.1	1.0	31.5	14.6	3.3	2.0	0.2	7.0	1.8
Loma El Huérfano N	2005	2.0	1.2	0.7	336	0	1.2	---	0.0	0.0	16.0	5.8	---	8.8	6.3	8.0	1.5
	2006	1.6	1.6	0.0	806	0	0.0	---	0.6	48.8	10.9	2.1	25.0	21.3	9.4	0.6	0.0
	2007	4.7	2.0	1.8	473	1	3.2	9.1	1.9	8.5	21.9	11.4	7.1	13.1	2.0	2.9	1.3
Loma El Huérfano S	2006	3.0	3.0	0.0	0	0	0.0	---	2.8	1.8	10.1	8.6	17.5	18.4	0.0	0.0	0.0
	2007	3.0	3.0	0.0	31	0	0.0	9.1	0.7	13.5	14.5	3.1	5.8	17.2	1.3	1.7	1.1
Los Bejucos S	2005	9.8	3.5	2.2	445	2	22.1	---	0.0	0.1	9.5	29.4	---	9.3	0.0	2.2	9.3
	2006	1.6	1.6	0.0	425	0	177.5	---	2.5	1.5	11.5	8.4	0.5	10.3	0.1	0.0	0.0
	2007	0.4	0.4	0.0	121	2	41.1	14.7	0.0	0.6	20.9	31.6	6.4	27.9	0.1	3.4	1.6
Los Bejucos SW	2006	3.8	3.8	0.0	461	0	496.7	---	2.7	0.2	22.4	3.4	0.5	19.2	0.0	0.1	0.0
	2007	9.4	2.5	3.3	89	2	509.4	8.1	0.0	0.9	27.1	19.8	3.7	26.3	0.0	3.5	0.6
Los Ratones E	2005	10.2	5.1	1.5	820	0	24.9	---	0.0	0.1	3.0	0.7	---	18.5	0.0	1.5	0.0
	2006	1.2	1.2	0.0	331	0	29.8	---	0.6	0.2	22.9	4.0	0.5	2.0	0.0	0.0	0.0

	2007	0.8	0.8	0.0	469	0	30.1	9.0	0.0	0.2	15.3	18.4	2.9	20.5	0.5	3.3	0.1
Los Ratones S	2005	5.5	2.3	1.7	602	0	0.0	—	0.0	0.3	10.8	0.7	—	10.7	0.0	2.3	0.0
	2006	2.3	2.3	0.0	541	0	0.0	---	1.1	0.0	25.9	3.8	0.5	1.9	0.0	0.0	0.0
	2007	8.2	4.3	1.0	161	2	0.0	10.8	0.0	0.0	20.3	23.2	2.1	10.5	0.3	6.1	0.1
Los Ratones SW	2006	2.7	2.0	0.6	0	0	1.3	—	5.2	0.3	23.1	0.3	0.5	2.4	0.1	0.0	0.0
	2007	4.7	1.2	3.0	0	0	5.1	9.2	1.1	0.0	34.9	1.9	2.1	6.3	0.4	1.6	0.0
Mata Ortiz	2005	2.7	2.0	0.8	375	0	0.0	—	0.0	0.0	11.7	2.5	---	8.9	0.4	6.1	0.2
	2006	0.8	0.8	0.0	438	0	0.2	—	1.1	0.0	23.6	0.0	0.5	1.9	0.4	0.2	0.0
	2007	4.3	2.3	1.2	121	0	0.1	7.7	0.0	0.0	40.4	6.1	2.1	6.1	0.3	5.3	0.6
Monteverde S2	2006	4.7	4.7	0.0	518	0	106.0	—	2.4	0.9	30.5	23.1	0.5	6.9	0.0	0.9	0.0
	2007	14.1	4.3	2.5	223	0	137.6	5.0	0.6	0.5	33.1	18.6	1.9	15.9	0.0	3.2	0.1
Monteverde SE	2005	1.0	1.0	0.0	8	3	0.1	—	0.0	0.0	19.7	1.6	—	6.0	4.9	19.8	0.0
	2006	1.5	1.5	0.0	38	2	0.1	—	1.8	13.8	22.3	6.3	40.0	13.9	12.6	3.9	0.0
	2007	3.9	2.0	1.2	31	1	1.8	13.1	1.6	7.6	20.4	9.8	6.5	8.9	4.4	7.5	0.0
Nifay SW	2006	0.4	0.4	0.0	459	0	31.3	—	1.2	1.8	33.1	13.4	12.5	20.6	0.5	0.0	0.0
	2007	0.0	0.0	0.0	40	0	64.4	18.1	0.2	1.1	22.2	54.9	6.1	26.4	6.3	4.1	0.2
Ojitos S	2006	2.7	2.7	0.0	375	0	678.2	—	2.7	8.0	51.8	6.7	12.5	15.1	2.1	0.0	0.0
	2007	0.0	0.0	0.0	250	0	843.9	11.7	0.6	10.8	30.6	18.2	5.2	16.0	5.8	7.9	0.8
Pancho Villa N1	2005	10.2	5.1	1.6	633	0	1.6	—	0.0	0.4	6.2	25.9	---	6.1	0.0	4.1	6.3
	2006	6.6	6.6	0.0	666	0	1.7	—	0.9	0.0	5.7	15.4	3.0	4.6	0.2	0.0	0.0
	2007	15.6	3.9	3.3	549	0	1.6	4.7	0.0	0.2	28.8	18.1	2.3	8.3	0.1	1.0	1.4
Pancho Villa N2	2006	1.2	1.2	0.0	622	0	0.0	---	3.9	6.9	25.6	2.8	7.5	6.1	0.0	0.3	0.0
	2007	0.0	0.0	0.0	357	0	7.2	9.2	0.2	6.2	35.6	19.8	3.9	17.8	5.1	9.9	3.0
Pancho Villa W	2006	3.5	3.5	0.0	934	0	132.3	---	2.7	0.3	11.9	1.3	0.5	0.7	0.0	0.3	0.0
	2007	2.3	1.2	1.3	335	0	110.6	3.9	0.0	0.0	33.2	4.1	2.4	6.4	1.2	6.2	0.0
Papalote de San Pedro	2006	9.8	9.8	0.0	1888	0	1.8	—	1.5	4.2	20.8	0.1	0.5	0.3	0.3	0.1	0.0
	2007	32.0	6.3	4.3	1290	0	8.5	12.2	0.0	35.7	13.8	6.7	2.1	13.0	0.8	6.5	0.1
Presa Casa de Janos	2005	8.2	4.3	1.2	492	0	138.1	—	0.0	0.1	30.4	14.5	—	10.9	0.1	8.9	2.0
	2006	3.5	3.5	0.0	853	0	106.1	—	0.9	0.5	20.4	8.8	3.0	13.2	0.3	0.3	0.0
	2007	14.1	3.5	3.1	402	0	158.7	23.0	0.0	7.4	11.7	44.2	4.4	35.9	0.9	6.0	2.2
Tierras Prietas	2005	9.0	3.1	2.5	313	0	0.0	—	0.0	0.0	33.1	0.6	—	13.9	0.0	2.4	0.0
	2006	2.3	1.6	1.0	291	2	0.0	—	0.3	0.0	18.1	0.1	0.5	0.3	0.0	1.1	0.0
	2007	2.0	0.8	2.0	424	0	0.0	5.5	0.1	0.9	32.9	8.7	1.6	3.4	0.3	3.4	0.1
Tres Alamos	2005	15.6	1.6	9.0	453	1	5.7	—	0.0	0.0	6.5	1.9	—	10.8	0.1	2.3	0.0
	2006	3.9	3.9	0.0	538	0	7.7	—	0.4	0.0	8.9	2.5	0.5	0.5	0.3	0.0	0.0
	2007	6.6	2.7	1.9	670	2	20.5	11.1	0.0	2.7	30.2	21.9	1.9	6.9	2.7	3.4	0.2

APPENDIX VII

Physical and landscape attributes of 45 sampling plots. CS = colony size, NC1 = number of colonies within 1 km, AC1 = area covered by BTPD colonies within 1 km, AH1 = area covered by hostile habitat within 1 km, DE = distance to edge, DR = distance to road, DT = distance to town, SD = soil density, Cl = soil clay content, Sa = soil sand content, OM = soil organic mater, pH = soil pH.

Plot name	CS	NC1	AC1	AH1	DE	DR	DT	SD	Sa	Cl	OM	pH
El Gavilán S	41.5	1	42.2	110.9	87	1756	990	2.383	69.0	22.0	1.30	7.7
Tres Alamos	12.3	0	12.3	67.7	87	833	3680	2.338	57.0	24.0	0.78	7.3
El Uno S1	19.0	1	21.7	55.0	51	142	4975	2.282	62.0	23.0	0.98	7.3
Los Ratones S	10.4	1	29.5	63.5	114	190	5280	2.430	76.0	17.0	0.39	7.5
Los Ratones E	7.5	1	8.6	109.8	59	114	5650	2.521	78.0	16.0	0.72	7.2
La Báscula W	2405.7	0	213.2	30.8	433	2772	4100	2.389	68.0	20.0	0.52	7.1
La Báscula E	2405.7	0	226.1	13.1	50	2105	4260	2.410	78.0	14.0	0.26	7.4
El Cuervo N	5247.5	0	254.3	171.3	461	3626	6000	2.498	80.0	8.0	0.99	6.8
El Cuervo E	5247.5	0	262.0	221.4	594	3650	5590	2.392	76.0	14.0	0.52	7.3
Tierras Prietas	255.0	0	112.6	89.7	98	364	1460	2.285	58.0	22.0	1.45	7.5
Buenos Aires	129.9	3	162.6	197.4	110	270	1700	2.413	76.0	13.0	0.78	7.1
El Apache	15.6	1	16.5	223.0	105	1092	8160	2.253	67.0	20.0	1.17	6.6
Los Bejucos S	43.2	0	42.3	5.6	50	241	2871	2.367	78.0	12.0	0.52	7.0
Pancho Villa W	45.8	0	40.2	18.2	110	2870	5974	2.374	76.0	10.0	0.65	7.3
Pancho Villa N1	309.9	0	149.8	197.6	236	1326	287	2,185	68.0	22.0	1.04	8.2
Ampliación Pancho Villa N	2405.7	0	209.4	5.6	202	2311	10655	2.259	60.0	30.0	1.04	8.3
El Toro	100.1	0	86.9	18.7	74	766	720	2.144	60.4	15.6	0.87	8.5
El Centro 1	3254.0	0	279.5	114.1	605	2050	2050	2.344	66.0	18.0	0.81	7.3
El Centro 3	3254.0	0	118.5	174.0	125	5320	4090	2.373	60.0	21.0	0.46	8.5
El Centro 2	3254.0	0	106.9	37.7	147	815	790	2.235	56.0	19.0	1.30	8.9
Monteverde SE	0.6	1	4.6	32.1	20	171	3510	2.425	78.0	15.0	1.10	8.1
Loma El Huérfano N	16.5	0	16.5	296.3	84	168	23630	2.259	50.0	20.0	0.78	8.5
Presa Casa de Janos	6.5	0	6.5	25.5	50	7000	6900	2.178	66.0	14.0	1.56	6.8
Mata Ortíz	71.3	0	58.1	11.0	79	4200	3900	2.330	64.0	23.0	1.30	7.0
El Aguila	303.4	0	98.0	52.7	128	182	5945	2.314	70.0	17.0	0.46	6.6
El Cuervo S1	7.5	0	7.5	2.5	86	95	920	2.326	60.0	20.0	0.41	7.3
El Cuervo S2	18.8	3	21.4	154.8	57	1680	2195	2.444	66.0	20.0	0.98	7.0
El Cuervo W	5247.5	0	114.2	5.0	50	1249	5860	2.446	73.0	14.0	0.46	7.2
Los Ratones SW	63.2	1	67.5	38.1	150	100	5830	2.413	68.0	19.0	0.26	7.7
Ampliación Pancho Villa S	2405.7	0	97.4	47.5	189	1086	9770	2.299	64.0	19.0	0.52	8.7
Nifay SW	43.2	0	43.2	177.9	189	109	7550	2.451	74.0	16.0	0.64	6.5
Ojitos S	246.7	0	135.7	43.5	146	7090	8666	2.281	67.0	16.0	0.91	6.3

Los Bejucos SW	7.1	3	13.6	18.5	35	101	1723	2.365	78.0	12.0	0.33	7.4
Agua Blanca	4.1	0	4.1	144.0	35	260	340	2.398	84.0	10.0	0.46	7.3
El Centro 4	3254.0	0	176.0	112.4	118	6450	6172	2.392	47.0	22.0	0.78	8.6
El Uno N	36.1	1	83.4	72.5	125	2078	3300	2.365	68.0	18.0	0.29	7.1
El Gavilán N1	56.6	1	64.0	225.2	35	2740	2580	2.372	56.0	26.0	0.78	7.0
Ampliación Pancho Villa E	2405.7	0	227.9	13.2	198	590	8270	2.332	56.0	25.0	0.93	7.7
Papalote de San Pedro	8.0	2	25.3	249.7	65	944	830	2.403	74.0	16.0	0.46	7.4
Monteverde S2	5.6	0	5.6	67.9	61	83	2570	2.307	44.0	37.0	0.17	7.4
Pancho Villa N2	309.9	2	85.6	52.8	94	138	1877	2.246	62.0	22.0	1.22	7.9
El Gavilán E	10.2	1	11.1	33.3	52	270	560	2.388	70.0	16.0	0.98	7.3
El Gavilán NE	1.6	1	1.9	64.7	27	1544	780	2.407	62.0	24.0	0.41	6.9
Loma El Huérfano S	2.9	0	2.9	148.9	57	525	22370	2.270	73.0	18.0	0.46	8.6
La Báscula-Pipa	2405.7	0	192.4	30.0	213	2580	4440	2.407	72.0	18.0	0.26	7.1

APPENDIX VIII

Pairwise correlation matrix for variables describing local and landscape attributes of 45 sampling plots. Bold numbers indicate correlations higher than 0.7. See Appendices VI and VII for variable abbreviations.

	CS	NC1	AC1	AH1	DE	DR	DT	Ct	Pr	Sh	HHR	DVR	UVR
CS	1.00	-0.37	**0.78**	0.04	0.68	0.38	0.04	0.04	0.06	-0.15	0.16	-0.07	-0.19
NC1	-0.37	1.00	-0.29	0.19	-0.29	-0.31	-0.26	0.11	0.06	0.15	0.14	0.12	0.11
AC1	**0.78**	-0.29	1.00	0.03	**0.78**	0.35	-0.05	-0.03	0.14	-0.13	0.13	-0.08	-0.25
AH1	0.04	0.19	0.03	1.00	0.21	-0.01	0.27	0.40	-0.18	0.00	0.05	-0.08	0.17
DE	0.68	-0.29	**0.78**	0.21	1.00	0.26	0.01	0.09	-0.07	-0.11	0.17	-0.07	-0.20
DR	0.38	-0.31	0.35	-0.01	0.26	1.00	0.06	0.16	-0.14	0.31	0.15	-0.09	-0.10
DT	0.04	-0.26	-0.05	0.27	0.01	0.06	1.00	0.00	0.03	0.08	0.01	0.04	0.15
Ct	0.04	0.11	-0.03	0.40	0.09	0.16	0.00	1.00	-0.08	0.16	0.05	0.03	0.15
Pr	0.06	0.06	0.14	-0.18	-0.07	-0.14	0.03	-0.08	1.00	-0.03	0.08	-0.02	-0.15
Sh	-0.15	0.15	-0.13	0.00	-0.11	0.31	0.08	0.16	-0.03	1.00	-0.04	0.06	0.05
HHR	0.16	0.14	0.13	0.05	0.17	0.15	0.01	0.05	0.08	-0.04	1.00	-0.13	0.06
DVR	-0.07	0.12	-0.08	-0.08	-0.07	-0.09	0.04	0.03	-0.02	0.06	-0.13	1.00	0.10
UVR	-0.19	0.11	-0.25	0.17	-0.20	-0.10	0.15	0.15	-0.15	0.05	0.06	0.10	1.00
FbR	0.22	0.09	0.22	0.03	0.18	0.15	-0.01	-0.03	0.05	0.27	-0.16	0.09	-0.19
GsR	0.08	0.01	0.15	0.07	0.13	0.08	0.00	-0.12	0.07	0.06	**0.84**	-0.24	-0.10
HHD	-0.09	-0.03	-0.12	0.12	-0.07	-0.06	0.30	-0.16	0.07	0.04	0.54	0.14	0.43
DVD	0.02	0.13	0.01	0.06	0.06	0.05	0.14	-0.10	0.09	0.18	0.59	-0.14	0.12
UVD	-0.19	0.08	-0.23	0.16	-0.12	-0.12	0.24	-0.11	0.05	0.26	0.25	-0.11	0.36
FbD	0.14	-0.02	0.14	0.08	0.16	0.13	-0.01	-0.07	0.13	0.11	0.40	-0.48	-0.10
GsD	0.04	0.11	0.17	0.17	0.11	0.05	-0.02	-0.11	-0.02	0.06	0.44	-0.27	-0.08
SD	0.22	0.28	0.09	0.09	0.12	-0.07	-0.15	-0.14	-0.01	-0.14	0.27	0.01	-0.15
Sa	0.04	0.24	0.06	-0.01	0.12	-0.11	-0.16	-0.16	0.03	-0.02	0.20	-0.06	-0.14
Cl	-0.15	-0.11	-0.08	-0.04	-0.12	-0.06	0.05	0.16	0.07	-0.07	-0.09	0.05	-0.01
OM	-0.11	-0.01	-0.05	0.02	-0.05	0.20	-0.06	0.17	0.09	0.07	0.06	-0.10	0.06
pH	0.16	-0.18	0.04	0.01	-0.08	-0.13	0.21	-0.07	0.08	-0.30	-0.42	0.05	0.16

APPENDIX VIII (cont)

	FbR	GsR	HHD	DVD	UVD	FbD	GsD	SD	Sa	Cl	OM	pH
CS	0.22	0.08	-0.09	0.02	-0.19	0.14	0.04	0.22	0.04	-0.15	-0.11	0.16
NC1	0.09	0.01	-0.03	0.13	0.08	-0.02	0.11	0.28	0.24	-0.11	-0.01	-0.18
AC1	0.22	0.15	-0.12	0.01	-0.23	0.14	0.17	0.09	0.06	-0.08	-0.05	0.04
AH1	0.03	0.07	0.12	0.06	0.16	0.08	0.17	0.09	-0.01	-0.04	0.02	0.01
DE	0.18	0.13	-0.07	0.06	-0.12	0.16	0.11	0.12	0.12	-0.12	-0.05	-0.08
DR	0.15	0.08	-0.06	0.05	-0.12	0.13	0.05	-0.07	-0.11	-0.06	0.20	-0.13
DT	-0.01	0.00	0.30	0.14	0.24	-0.01	-0.02	-0.15	-0.16	0.05	-0.06	0.21
Ct	-0.03	-0.12	-0.16	-0.10	-0.11	-0.07	-0.11	-0.14	-0.16	0.16	0.17	-0.07
Pr	0.05	0.07	0.07	0.09	0.05	0.13	-0.02	-0.01	0.03	0.07	0.09	0.08
Sh	0.27	0.06	0.04	0.18	0.26	0.11	0.06	-0.14	-0.02	-0.07	0.07	-0.30
HHR	-0.16	**0.84**	0.54	0.59	0.25	0.40	0.44	0.27	0.20	-0.09	0.06	-0.42
DVR	0.09	-0.24	0.14	-0.14	-0.11	-0.48	-0.27	0.01	-0.06	0.05	-0.10	0.05
UVR	-0.19	-0.10	0.43	0.12	0.36	-0.10	-0.08	-0.15	-0.14	-0.01	0.06	0.16
FbR	1.00	0.01	0.00	0.05	0.04	0.16	0.05	0.04	0.02	-0.05	0.02	-0.24
GsR	0.01	1.00	0.01	0.54	0.24	0.17	0.32	0.05	0.00	0.10	-0.01	-0.23
HHD	0.00	0.01	1.00	0.33	0.50	0.05	0.08	-0.11	-0.01	-0.11	0.17	0.22
DVD	0.05	0.54	0.33	1.00	0.27	0.06	0.09	0.03	-0.03	-0.01	0.12	-0.14
UVD	0.04	0.24	0.50	0.27	1.00	0.23	0.05	-0.05	-0.03	-0.04	0.13	-0.05
FbD	0.16	0.17	0.05	0.06	0.23	1.00	0.31	-0.01	0.12	-0.09	0.12	-0.05
GsD	0.05	0.32	0.08	0.09	0.05	0.31	1.00	-0.03	0.14	-0.18	0.07	-0.10
SD	0.04	0.05	-0.11	0.03	-0.05	-0.01	-0.03	1.00	0.53	-0.34	-0.44	-0.38
Sa	0.02	0.00	-0.01	-0.03	-0.03	0.12	0.14	0.53	1.00	**-0.78**	-0.23	-0.40
Cl	-0.05	0.10	-0.11	-0.01	-0.04	-0.09	-0.18	-0.34	**-0.78**	1.00	0.12	0.24
OM	0.02	-0.01	0.17	0.12	0.13	0.12	0.07	-0.44	-0.23	0.12	1.00	0.07
pH	-0.24	-0.23	0.22	-0.14	-0.05	-0.05	-0.10	-0.38	-0.40	0.24	0.07	1.00